644

Department of Agriculture

Forest Service

Cooperative State Research Service

Agriculture Handbook No. 644

Spruce Budworms Handbook

Predators of the Spruce Budworm

best copy available

A 1.76:

In 1977, the United States Department of Agriculture and the Canadian Department of the Environment agreed to cooperate in an expanded and accelerated research and development effort, the Canada/United States Spruce Budworms Program (CANUSA), aimed at the spruce budworm in the East and the western spruce budworm in the West. The objective of CANUSA was to design and evaluate strategies for controlling the spruce budworms and managing budworm-susceptible forests to help forest managers attain their objectives in an economically and environmentally acceptable manner. The work represented in this publication was wholly or partially funded by the Program. This manual is one in a series on the spruce budworm.

canusa

Canada
United States
Spruce Budworms
Program

READEX
FICHE

November 1985

Contents

Introduction 1
Life History of the Spruce Budworm 2
Host Trees 2
Susceptibility of Life Stages to Predation 3
Predator Groups 5
Overview of Predators 5
Predators of Eggs 6
Phalangids 6
Mites 6
Spiders 8
Plant Bugs 10
Lacewings 10
Beetles 10
Ants 11
Birds 12
Predators of Small Larvae 13
Phalangids 13
Spiders 14
Beetles 17
Ants 17
Miscellaneous Insects 18
Birds 18
Predators of Large Larvae 19
Spiders 19
Dragonflies 20
Beetles 21
Spruce Coneworms 24
Ants 25
Wasps 27
Fish 30
Mammals 30
Birds 31
Predators of Pupae 34
Spiders 34
Beetles 34
Spruce Coneworms 35
Budworm Larvae 37
Syrphids 37
Ants 37
Mammals 38
Birds 38

Predators of Adults 41
Spiders 42
Dragonflies 45
Beetles 45
Robber Flies 46
Ants 47
Birds 48
Predators as Natural Regulators 49
Endemic Spruce Budworm Populations 52
Epidemic Spruce Budworm Populations 56
Methods for Studying Predation 56
Exclusion Techniques 57
Direct Assessments 57
Serological Tests 57
Radioisotope Tagging 58
Direct Observations 59
Conservation and Enhancement of Predators 59
Habitat Requirements 59
Food Requirements 60
Nesting Requirements 61
Summary 62
Acknowledgments 62
Selected References and Guides for Identifying Predators 62
Phalangids 62
Spiders 63
Mites 63
Dragonflies 63
Carabid Beetles 63
Coneworms 64
Robber Flies 64
Ants 64
Wasps 64
Fish 64
Birds 64
Mammals 65
Literature Cited 65

Predators of the Spruce Budworm

by Daniel T. Jennings and
Hewlette S. Crawford, Jr.[1]

Introduction

The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is the most destructive forest insect pest in eastern North America. Millions of acres of spruce–fir forests have been damaged by the spruce budworm in eastern Canada and in the North-central and Northeastern United States from Minnesota to Maine. Recorded outbreaks of the budworm date back to the early 1700's; but in the 20th century, outbreaks are increasing in frequency, extent, and severity (Blais 1983).

The spruce budworm is a native, natural component of the spruce–fir forest. Managers need to know how to manage the insect to prevent or minimize damage to the forest. Applied control of the spruce budworm has been largely chemical. A more integrated approach is needed that includes safer, longer lasting, less costly methods of pest management. Such methods should be compatible with multiple uses of all forest resources, including fiber, wildlife and fish production, soil and water conservation, and recreation.

The spruce–fir forest has various natural agents that help keep budworm populations in check between outbreaks. These natural agents of control, also called natural enemies, include various diseases, parasites, and predators.

Enhancement of predators of the spruce budworm is a desirable feature of integrated pest management; however, before we can incorporate predator enhancement we need to know which predators are important, how effective they are in regulating budworm populations, and what their habitat requirements are. Ultimately, such information and understanding will lead to the identification and development of forest-management strategies that enhance predators of the spruce budworm.

The goals of this handbook are to (1) review available information on predators of the spruce budworm; (2) provide information on predator biologies, including life stages, modes of attack, and general importance; (3) summarize the importance of predators and predation in population dynamics of the spruce budworm; (4) review forest-management practices that enhance predator populations; and (5) list basic literature sources for identifying predators of the spruce budworm.

[1]Daniel Jennings is a research forest entomologist with the USDA Forest Service, Northeastern Forest Experiment Station, Orono, ME. Hewlette Crawford, Jr., is a research wildlife biologist with the Station at Amherst, MA.

Life History of the Spruce Budworm

The spruce budworm has four life stages: egg, larva, pupa, and adult. The adult stage is a moth with a wingspan of about three-quarters of an inch (2 cm). The female moths lay their eggs in masses on needles of host trees in mid-July to early August. The number of eggs per mass varies considerably but averages about 20. The eggs hatch in about 8 to 12 days, and the newly emerged first-instar larvae do not feed but disperse and seek overwintering sites under bark scales and in old staminate flower bracts. After spinning a silken hibernaculum, the larva molts to the second instar, enters diapause, and overwinters.

In the spring of the following year, the second-instar larvae emerge from their hibernacula, disperse, and seek feeding sites. Newly opened staminate flowers are the preferred food on balsam fir, *Abies balsamea* (L.) Miller, during the initial feeding stage. When staminate flowers are not available and vegetative buds are "tight" and unexpanded, larvae mine the previous year's needles. Usually, only one needle is mined and the larva molts to the third instar within or soon after leaving the needle. By mid- to late May or early June, depending on temperatures, most of the larvae leave mined needles and begin feeding on newly opened vegetative buds (Miller 1963a).

Feeding continues on the new foliage of developing shoots and on old foliage once the current foliage is consumed. The larvae typically web two or more shoots together to form a feeding tunnel or shelter. During this active feeding period, the larvae molt three more times to reach the sixth instar by late June or early July. The fifth and sixth instars cause most of the feeding damage to host trees. Destruction of current shoots causes considerable larval movement, and many larvae drop from their host trees and are exposed to ground-inhabiting predators.

After development, the larva stops feeding and transforms into a pupa. The pupal stage lasts about 10 days, after which the moth emerges. The female moth emits a sex pheromone that attracts the male for mating. Moths live about 2 weeks and are found from early July to August. Shortly after mating, the female moth begins to lay eggs, completing the life cycle. There is only one generation of the spruce budworm per year, but the life cycle spans 2 calendar years.

Host Trees

Balsam fir is the principal host of the spruce budworm in eastern North America; it is the host that suffers the greatest damage and tree mortality (Miller 1963a). Outbreaks are most likely when mature stands of balsam fir cover extensive areas (Blais 1983). The budworm also attacks and feeds on white spruce, *Picea glauca* (Moench) Voss; red spruce, *P. rubens* Sarg.; black spruce, *P. mariana* (Mill.) B.S.P.; and blue spruce, *P. pungens* Engelm. During

outbreaks there may be feeding on tamarack, *Larix laricina* (Du Roi) K. Koch; eastern white pine, *Pinus strobus* L.; and eastern hemlock, *Tsuga canadensis* (L.) Carr. Mature and overmature trees are most susceptible to attack, though trees of all sizes can be damaged or killed during an epidemic.

Susceptibility of Life Stages to Predation

All life stages of the spruce budworm are susceptible to attack by predators. However, some stages are more susceptible than others. For example, during both larval dispersal periods, the small larvae are exposed and subject to attack by arboreal and epigeal predators. Once needle or bud mining begins, the larvae are protected and are less likely to be eaten by predators. Overwintering larvae in hibernacula are protected but not immune to predation.

Many predators rely on movements to detect potential prey. Because egg masses are deposited on needles and are relatively stable, the egg masses are not likely to be detected except by foliage-searching predators such as coccinellid beetles and birds.

Large larvae of the spruce budworm may escape foliage-searching predators by dropping from their host trees. This dropping behavior may have survival value; but dropping also exposes the larvae to other predators (fig. 1), especially when the larvae drop to nonhost vegetation or to the forest floor, where ants, carabid beetles, spiders, and small mammals often are numerous.

Conversely, the inability to move and escape predators increases the susceptibility of pupae to predation. Pupae generally are found near the apexes of branches in silken shelters constructed by the larvae before pupation. Although capable of wiggling and squirming, pupae usually remain attached to these silken threads by means of cremaster hooks.

Spruce budworm moths may escape some predators by taking flight; however, flying moths are exposed to aerial-searching predators such as dragonflies, robber flies, and birds. There are temporal and sexual differences in susceptibilities of moths to predation. Male spruce budworm moths are more active, rapid fliers than female moths. Female moths must lay some of their eggs before engaging in long-distance flights. Moths are subject to predation by foliage-searching predators such as birds and spiders. During coitus, both sexes are susceptible and vulnerable to attack because they represent a relatively large target and their movements are somewhat impaired.

Habitats occupied by the different life stages of the spruce budworm and searching behaviors of potential predators also influence prey susceptibility. Most spruce budworm eggs are deposited on peripheral shoots in the upper crowns of host trees (Miller 1958, 1963a). Such sites are exposed

Figure 1—Cape May warbler and dropping spruce budworm larva.

to predators that concentrate their searches near branch apexes. After egg hatch, the young larvae disperse, some falling to lower crown levels, where other predators are found. The small larvae also disperse to nearby trees, nonhost vegetation, and the forest floor. During dispersal the larvae are exposed to numerous arboreal and epigeal predators.

Similarly, large larvae dropping from tree crowns are susceptible to predators. Large larvae falling to intervening vegetation or the forest floor are especially vulnerable to attack by ants and spiders.

Starvation also contributes to movement of large larvae, and movement both within and between tree crowns exposes the larvae to a variety of predators.

Although all life stages of the spruce budworm are susceptible to predation, susceptibilities vary according to life stage, location, and behavior of both predator and prey.

Predator Groups

Predators of the spruce budworm include both invertebrates and vertebrates. The largest guilds of invertebrate predators are found among the insects and spiders. With few exceptions, most of the insect orders (Coleoptera, Hymenoptera, Diptera, etc.) contain predaceous species; all spiders are predaceous.

Vertebrate predators of the spruce budworm include birds, mammals, and fishes. Birds are the best-known and probably most important predators of the spruce budworm. Predaceous mammals include the rodents (Rodentia) such as voles and the insectivores (Insectivora) such as shrews. Vertebrates have a high attack potential because they are warm blooded and have relatively high metabolic rates that require ample food supplies.

Overview of Predators

In this section we review what is generally known about predators of the spruce budworm. This review is restricted largely to predators of *Choristoneura fumiferana*, though reference is made to the jack pine budworm (*C. pinus* Freeman) and the western spruce budworm (*C. occidentalis* Freeman).

We have taken the life-table approach, presenting what is known about predators of each prey life stage, beginning with the egg stage and progressing to the adult or moth stage. This approach introduces some overlap among the predators because some predator groups (birds, spiders) prey on all life stages of the spruce budworm. And within each predator group, some species probably are more important than others as predators. Predators of large larvae and pupae of the spruce budworm are most important in terms of generation survival (Morris 1963).

Predators of Eggs

Despite an extensive review of the spruce budworm literature and efforts to collate unpublished information from colleagues, our knowledge and understanding of this complex predator–prey system remains incomplete. Certainly, not all of the predators and potential predators of the spruce budworm have been identified or studied. For example, virtually nothing is known about the reptiles and amphibians that possibly attack and feed on spruce budworms. And nocturnal-flying bats are potential predators of spruce budworm moths, but they remain unstudied in northeastern spruce–fir forests. Perhaps the scarcity of information about some predator groups will help stimulate future investigations.

Predators of spruce budworm eggs include phalangids, mites, spiders, plant bugs, lacewings, beetles, ants, and birds.

Phalangids

Little is known about these predatory arachnids and their food habits. Some species are scavengers and feed on dead insects (Todd 1950); others are predaceous and feed on lepidopterous larvae, pupae, and adults (Bishop 1949, Edgar 1971). Presumably, they also attack and feed on lepidopterous eggs, including eggs of the spruce budworm. Neilson (1963) recognized only two groups (mites and insects) as predators of budworm eggs; Varty and Titus (1974) included phalangids among the arthropods that influence budworm abundance in the egg stage. However, virtually nothing is known about their specific egg-feeding habits.

In Maine, significantly more individuals and species of phalangids were trapped in uncut residual strips and in dense spruce–fir stands than in clearcut strips (Jennings et al. 1984). Peaks in seasonal activities of phalangids coincided with the egg and early-larval stages of the spruce budworm. Because budworm eggs are relatively small and immobile, we suspect they are susceptible to predation by phalangids.

Mites

Mites (Arachnida: Acari) are among the most abundant arthropods in ter-

restrial ecosystems. They rival insects in numbers of species and habitats occupied (Borror et al. 1976). Many are parasitic; others are predaceous, phytophagous, or scavengers. They are of considerable biological interest and importance (Treat 1975).

Both parasitic and predaceous mites attack the spruce budworm. Parasitic mites infesting spruce budworm moths may indirectly affect budworm egg production by reducing fecundity (Houseweart et al. 1980).

Most of our knowledge about predaceous mites concerns mites feeding on budworm eggs. Bennett (1952a) reported that *Anystis agilis* was observed preying on budworm eggs in New Brunswick. Neilson (1963) noted that mite populations were estimated during foliage examinations for budworm eggs; the most common species was *A. agilis* Banks.

Morris (1963) reported that egg predation of the spruce budworm was caused largely by mites (species undetermined). Red mites frequently were observed feeding on eggs in the Green River area of New Brunswick, and mites were extremely abundant during the budworm's egg-laying period.

These observations of mite predation on budworm eggs prompted further investigations by Loughton et al. (1963). "Known-feeding" tests with red mites in the laboratory showed that mites consumed an average of 0.68 budworm egg per day, with an average interval between feedings of 2.3 days. Individual mites consumed as many as five eggs in 1 day, and feeding generally was irregular.

Serological tests for detecting predation in natural populations showed that 22 to 24 percent of the mite population sampled in the Green River area had fed on spruce budworm eggs. Loughton et al. (1963) concluded that this level of mite predation was of considerable significance because mites commonly fed on two or more eggs. The serological test detected egg proteins in mites for only 24 hours after feeding; thus, total predation by mites may have been underestimated.

In New Brunswick, Varty (1977) observed predaceous mites feeding on budworm eggs and on aphids, scales, collembola, and other mites. Populations of mites were very high in August and were estimated at 404,695 per acre (1 million/ha). He noted that at least eight species of predaceous mites (mostly trombidiform taxa) are found on balsam fir in New Brunswick.

In July 1979, David M. Kendall of our staff observed red mites feeding on green, unhatched eggs of the spruce budworm in Washington County, ME. The eggs were laid on small understory balsam fir. The mites were later determined to be an undescribed species of *Balaustium* (Family Erythraeidae). We have subsequently made additional collections of *Balaustium* mites from

balsam fir foliage examined for spruce budworm egg masses.

Mites (fig. 2) show both numerical and functional responses to increases in budworm prey density. On the Green River Watershed, Neilson (1963) noted that mite populations showed numerical responses to egg densities over the entire range of densities studied. He concluded that these numerical responses may partially explain the increase in percent predation observed with increasing egg density up to 9.3 eggs per ft^2 (100 eggs/m^2) of foliage. Mites also showed functional responses, i.e., numbers of eggs consumed per mite increased with egg density, especially at prey densities below 9.3 eggs per ft^2 of foliage.

Spiders

Spiders (Arachnida: Araneae) are among the most abundant predaceous arthropods in northeastern spruce–fir forests. Morris (1963) estimated populations of 75,000 spiders per acre (185,325/ha), not including species that restrict their hunting to the ground or to low vegetation. This estimate probably is conservative because some of the more active forms escape during collection of foliage samples. Varty (1980) reported average spider densities of 0.4 to 0.8 individual per ft^2 (5 to 10 individuals/m^2) of branch surface; occasionally, there were as many as 242,817 per acre (600,000/ha) of balsam fir.

Spiders generally feed on mobile prey, chiefly insects. They use two principal methods of prey capture: web building and hunting. Both methods involve visual and tactical cues triggered by mobile, flying, or walking insects. Few spiders have been observed feeding on immobile prey and even fewer on insect eggs.

Morris (1948) reported that several species of spiders found on mature balsam fir trees in New Brunswick prey on both larvae and eggs of the spruce budworm. The spiders were not identified. Both Neilson (1963) and Loughton et al. (1963) concluded that spiders usually do not attack immobile prey because in cage experiments spiders could not be induced by starvation to prey on budworm eggs. Hence, spiders were not tested with antiegg sera to determine predators of budworm eggs.

In 1977, a jumping spider, *Metaphidippus flavipedes* (G. & E. Peckham), was observed feeding on a green, uneclosed egg mass of the spruce budworm (Jennings and Houseweart 1978). The egg mass was deposited on foliage of a young understory balsam fir. The spider was disturbed and the feeding was interrupted; however, once the eggs hatched, the spider readily captured and fed on the first instars.

The extent of spider predation on budworm eggs is not known; we suspect that it is minor.

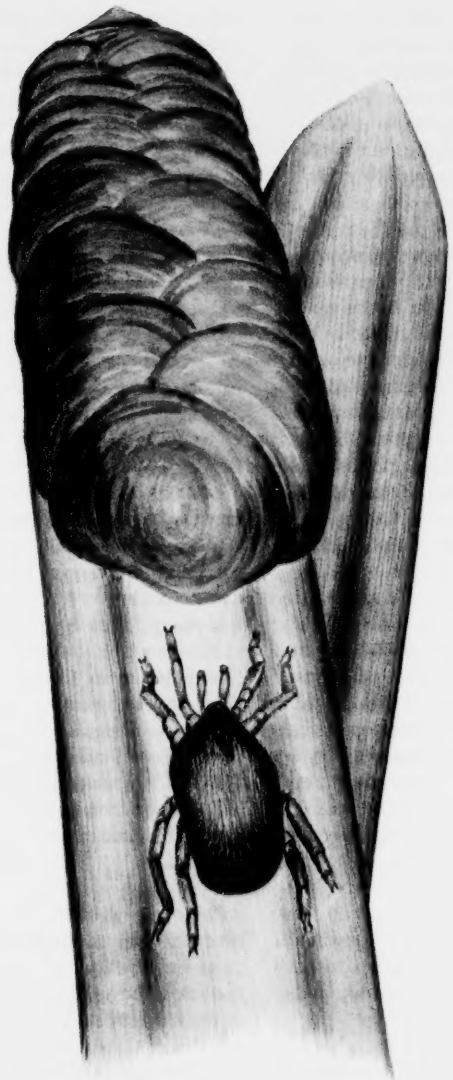

Figure 2—Red mite, *Balaustium* sp., preying on spruce budworm eggs.

Plant Bugs

Plant or leaf bugs (Insecta: Hemiptera) belong to the family Miridae, the largest group of true bugs. Most mirids feed on the juices of plants, but a few prey on other insects.

During investigations of budworm predators on the Green River Watershed, New Brunswick, mirids were recognized as possible predators of budworm eggs (Dominion Department of Agriculture 1950). However, little is known about the species associated with northeastern spruce–fir forests and their importance as predators of spruce budworm eggs. Presumably, the prey is sucked dry, leaving little evidence of predator activity.

Lacewings

Lacewings (Insecta: Neuroptera) are small, soft-bodied insects with four membranous wings. The wings usually have a great number of cross veins and extra branches of the longitudinal veins; hence, the order name (Borror et al. 1976). The front and hind wings are held rooflike over the body.

Larval and adult neuropterans live in a variety of habitats, and many are predaceous. The adults are weak fliers, but most are predaceous and feed on relatively weak prey.

Neilson (1963) reported that larvae of Neuroptera (species undetermined) had been observed eating eggs of the spruce budworm. Most likely these were brown lacewings (Family Hemerobiidae) or green lacewings (Family Chrysopidae); the larvae of both families are predaceous. Brown lacewings generally are found in wooded areas; green lacewings are common in grass and weeds and on the foliage of trees and shrubs (Borror et al. 1976).

Virtually nothing is known about the importance of neuropteran predation on spruce budworm eggs. The Neuroptera associated with spruce–fir trees have scarcely been studied.

Beetles

Beetles (Insecta: Coleoptera) are the largest order of insects; over a quarter million species have been described (Borror et al. 1976). These insects are found in almost every kind of available habitat. Their feeding habits are varied; many are phytophagous, many are predaceous, some are scavengers, and others feed on mold and fungi. The beetle families Carabidae, Staphylinidae, and Coccinellidae contain members that are predaceous, both as larvae and adults.

At least two species of ladybird beetles (Family Coccinellidae) are known to feed on eggs of the spruce budworm. In cage experiments, adults of the ladybeetle *Mulsantina hudsonica* (Casey) readily accepted budworm eggs as prey (Varty 1969). This small brown coccinellid is the most abundant ladybeetle on balsam

fir in New Brunswick. It feeds mainly on the balsam twig aphid, *Mindarus abietinus* Koch, but eggs and early-instar larvae of the spruce budworm are subject to predation.

Adults of *Anatis mali* (Say) have been observed in Maine feeding singly and in groups of three to four on newly deposited egg masses of the spruce budworm. Field and laboratory studies indicate that the life history of *A. mali* is well synchronized with the ovipositional period of the spruce budworm.[2] Egg masses of the spruce budworm are deposited over a period of about 27 days beginning in late June or early July (Houseweart et al. 1982). The last 2 weeks of the coccinellid's larval period coincides with the beginning of the budworm's egg period. Newly emerged *A. mali* adults are present for about 3 weeks of the spruce budworm's egg-mass period.

During investigations of the spruce budworm on the Green River Watershed in New Brunswick, Neilson (1963) noted that larvae of Coccinellidae (species undetermined) were observed feeding on budworm eggs (fig. 3).

Little is known about the predatory beetle fauna associated with northeastern spruce–fir forests. Few studies have dealt with the beetles found on various budworm host-tree species. In addition to *M. hudsonica*, Varty (1969) listed the following six species of coccinellids found on balsam fir in New Brunswick: *Anatis mali* (Say), *Adalia bipunctata* (L.), *A. frigida* (Schn.), *Coccinella monticola* Mulsant., *Chilocorus stigma* (Say), and *Coccinella transversoguttata* Falderman. Little is known about the food habits of most of these coccinellids.

Ants

Ants (Hymenoptera: Formicidae) are the most widely distributed of the social insects (Francoeur 1979); often they are locally abundant in forest habitats, including northeastern spruce–fir forests that are infested with the spruce budworm.[3] Ant activity begins early in the spring and continues into midfall. Their feeding habits are diverse: some species are carnivorous; others are herbivorous. Many feed on sap, nectar, and honeydew secretions; and many are able to switch their diets to take advantage of abundant foods, such as lepidopterous defoliators. Because ants prey on numerous species of forest pests, they are considered potentially important as agents of population mortality.

Although we have no direct observations of ants preying on spruce budworm eggs, we strongly suspect that

[2]Lawrence, Robert K.; Houseweart, Mark W.; Jennings, Daniel T. *Anatis mali* (Say), a coccinellid predator of spruce budworm egg masses. [Unpublished manuscript.]

[3]Jennings, Daniel T.; Houseweart, Mark W.; Francoeur, Andre. Ants (Hymenoptera: Formicidae) associated with strip clearcut and dense spruce–fir forests of Maine. [Unpublished manuscript.]

Figure 3—Coccinellid beetle, *Anatis mali*, preying on spruce budworm eggs.

budworm eggs are subject to ant predation. Finnegan (1974) noted that predation by ants was not limited to a particular prey life stage; ants prey on eggs, larvae, pupae, cocoons, and adults. Varty and Titus (1974, p. 17) included ants among the arthropods that "exercise a light restraint on budworm abundance in the egg and small-larval instars. . . ." However, they gave no quantitative data.

In northern Maine, peaks in pitfall catches of ants coincided with the egg stage of the spruce budworm, particularly in dense spruce–fir stands.[3] Captured ants included individuals and species that forage in nearby tree crowns.

Birds

All life stages of the spruce budworm are subject to predation by birds; however, little is known about birds preying on budworm eggs. George and Mitchell (1948) reported that the larvae, pupae, adults, and eggs of the spruce budworm provide excellent food for insectivorous birds but gave no specific information about species preying on eggs. Neilson (1963) concluded that budworm egg masses are too small to constitute worthwhile

prey for birds, and Morris (1963) surmised that wood warblers probably do not prey on budworm eggs since the warblers did not accept small larvae as prey.

During our bird studies in Maine, we collected an adult male pine siskin, *Carduelis pinus* (Wilson), that had fed on egg masses of the spruce budworm (Jennings and Crawford 1983). Only new, unhatched egg masses were eaten by the pine siskin, and individual eggs destroyed by one bird totaled 2,162. Apparently the bird stripped the egg masses from host-tree needles because there were no needles or fragments of needles in the crop or gizzard.

Egg predation by birds is one source of mortality not recognized or accounted for in conventional life tables (Morris 1963). Such mortality is difficult to detect and evaluate because the egg masses and eggs are removed and consequently are "missing" from the population.

Predators of small larvae (L_1–L_2) of the spruce budworm include phalangids, spiders, beetles, ants, miscellaneous insects, and birds.

Phalangids

Varty and Titus (1974) included phalangids among the arthropods that exercised a light restraint on budworm abundance in the egg and small-larval stages. However, they concluded that phalangids have virtually no importance in the survival of large larvae, pupae, or adult budworms. No doubt, this conclusion is based on the general inability of phalangids to subdue large, active prey.

A determination of the phalangid fauna associated with northeastern spruce–fir forests has received more attention than their predatory roles. Carter and Brown (1973) reported six species—*Caddo agilis* Banks, *Sabacon crassipalpe* (L. Koch), *Odiellus pictus* (Wood), *Leiobunum calcar* (Wood), *L. bicolor* (Wood), and *L. ventricosum* (Wood)—from pitfall traps in a mature red spruce stand in New Brunswick. Five of these species, all except *L. bicolor*, were collected in budworm-infested spruce–fir stands of New Brunswick by Varty and Carter (1974). Because of misidentification and nomenclatural change, *S. crassipalpe* is no doubt *S. cavicolens* (Packard) and *L. bicolor* is *L. elegans* (Weed).

Five genera and at least seven species of phalangids were collected by pitfall

traps in strip-clearcut and dense spruce–fir forests of northern Maine (Jennings et al. 1984). More than 90 percent of the specimens were *Leiobunum calcar* (Wood). The phalangids generally preferred the more closed, shaded habitats of dense spruce–fir stands and of uncut residual strips to the more open, cleared habitats of cut strips. Significantly more individuals and species were trapped in uncut residual strips and in dense spruce–fir stands than in clearcut strips. For both study years, phalangids were most abundant and mean catches per pitfall trap were greatest during the egg and first-instar periods of the spruce budworm. The egg and early-larval instars probably are the stages most susceptible to attack and predation by phalangids. Strip clearcutting contributes to dispersal losses of early-instar larvae (Jennings et al. 1983), exposing the larvae to numerous predators including phalangids (fig. 4).

Special techniques are needed to determine the predator–prey relationships involving phalangids. Loughton et al. (1963) included phalangids among the predators that could be assessed serologically for their predation on spruce budworm.

Spiders

Spiders are opportunistic predators that feed on a variety of prey, including lepidopterous larvae. Johannsen (1913) first noted that spiders prey on first instars of the spruce budworm in Maine. He observed spiders preying on budworm larvae, both in the laboratory and in the field, shortly after the larvae emerged from egg masses. Five species of spiders, all web spinners, were collected from spruce foliage on which egg masses of the spruce budworm were abundant. He concluded that "two spiders . . . were quite capable of exterminating the several hundred newly hatched little larvae which emerged from the dozen or more egg masses," placed on a caged balsam fir in the laboratory (Johannsen 1913, p. 24).

Tothill (1923) included spiders among the "checks" causing mortality to budworm progeny. In New Brunswick in 1918, he estimated that of the 150 eggs laid by the typical budworm, 8 of the resulting larvae (5.3 percent) would be eaten by spiders, but he gave no indication of the species or prey larval size.

During investigations on the Green River Watershed, New Brunswick, F. C. Hirtle observed several species of spiders preying on both budworm larvae and eggs (Morris 1948). The species were not identified, but populations averaged 20 per mature balsam fir tree.

In New York, Jaynes and Speers (1949) placed 1,100 first-instar larvae of the spruce budworm on a 6-ft (1.8-m) balsam fir. They commonly observed spiders seizing larvae as the larvae spun down from one branch to another; however, no exact count of

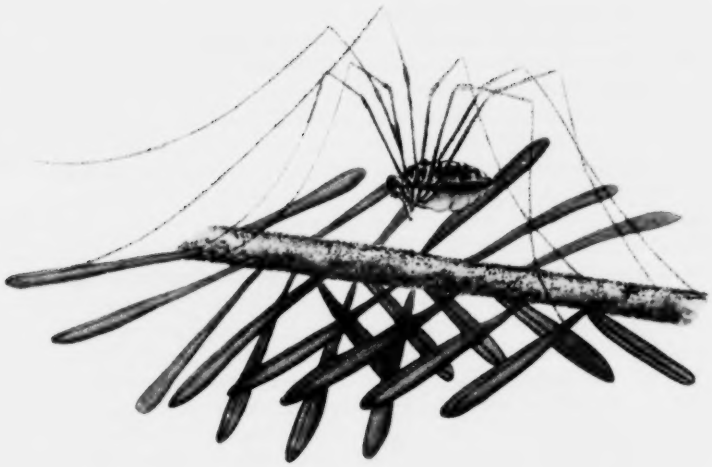

Figure 4—Phalangid feeding on first-instar spruce budworm.

mortality was made. The spiders were not captured and identified.

Conversely, Miller (1958) concluded that very few early instars fall prey to spiders or to other predators. Apparently, this conclusion was based on earlier observations (Bennett 1952b) where spiders were confined in jars or cages and potential prey larvae were introduced. Only *Grammonota* sp. was observed preying on a larva. In some instances, the budworm larvae had spun webbing that the spiders did not disturb.

Hirtle (1951) concluded that spiders probably are important predators of the budworm during the early-larval instars. Mott (1963) noted that predation by spiders takes place during dispersal of first and second instars but that little is known about its importance. In New Brunswick, Morris (1963) noted that spiders generally were active from early May, before larval emergence from hibernacula, until early November. Spiders were abundant and active during both egg hatch and dispersal of first instars (Morris) 1963.

Loughton et al. (1963) gives some indication of the magnitude of spider predation on small budworm larvae. Using serological techniques and antisera prepared against first and second instars, they found that 13 and 7 percent of the spiders collected during the springs of 1959 and 1960 had fed on spruce budworm larvae. These percentages were based on field collections made between larval emergence and needle mining; predation dropped as expected during needle mining. With the appearance of first-instar larvae in July, spider predation was estimated to be at about the same level as before pupation, i.e., in 1959, 26 percent of the spiders had fed on early-instar larvae; similarly, 25 percent had fed on early instars in 1960.

These investigators noted that proteins (antigens) of first- and second-instar larvae were detectable for only 1 day after feeding by spiders; hence, estimates of field predation are conservative. Small larvae of the spruce budworm were consumed at more frequent intervals than large larvae, and more small larvae were eaten. Confined species offered 10 first-instar larvae averaged 7.5 to 9 larvae consumed per day over a 4-day period (Loughton et al. 1963).

In laboratory studies on the predatory behavior of *Grammonota angusta* Dondale, a species frequently found on conifer foliage in New Brunswick, Haynes and Sisojevic (1966) found that the spider attack rate was proportional to prey density up to eight second-instar larvae. They noted that *G. angusta* is well adapted to take advantage of prey that are extremely abundant for only a short time, e.g., the situation during larval dispersal. The spider is very resistant to starvation.

Renault and Miller (1972) designed and conducted field experiments to assess the predatory behavior of *Dictyna phylax* Gertsch and Ivie, a small web-building spider, on emerging spruce budworm larvae in the spring. In these experiments, second-instar larvae were "planted" on branches of balsam fir trees, some with *D. phylax* juveniles and adults and some spider-free. Results over a 3-year period showed that 60 percent of the larvae survived on the control foliage, whereas only 3 percent survived on foliage with a spider predator. The authors concluded that *D. phylax* is extremely efficient in capturing small spruce budworm larvae that are attempting to establish feeding sites at the tips of branches.

Laboratory feeding tests showed that partially starved *D. phylax* females consumed an average of 15 second-instar larvae in a 6-hour period before changes were noted in attack response, handling time, and utilization of prey (Renault and Miller 1972). The web of this dictynid spider is spun near the periphery of spruce and fir branches, ideal sites for capturing migrating first- and second-instar spruce budworm larvae. However, the authors concluded that the probability of a predator–prey en-

counter was extremely low at endemic budworm densities.

In northern Maine, the jumping spider *M. flavipedes* was observed capturing and feeding on first-instar larvae of the budworm after the larvae emerged from eggs (Jennings and Houseweart 1978).

Beetles

Our knowledge of beetles preying on early instars of the spruce budworm is very limited. Because the larvae are small, mobile, and somewhat secretive, observations of predators feeding on them are rare. During dispersal, which occurs in both first and second instars, larvae are subject to predation by arboreal and epigeal predators, including predaceous beetles.

Varty (1969) noted that hungry adults of the coccinellid beetle *M. hudsonica* Casey may prey on second-instar budworms when the budworms leave their hibernacula in early May. He concluded that if a large population of hungry ladybeetles occupies the same habitat as the migrating budworm larvae, there is a prospect for significant pest mortality.

In northern Maine, seasonal activity of carabid beetles (including predaceous species) was greatest during the early- and late-larval stages of the spruce budworm.[4] Activity generally declined as the summer progressed, but carabid beetles were abundant during spring dispersal of the first instars in July. Strip clearcutting contributes to dispersal losses of these early-stage larvae (Jennings et al. 1983) by exposing the larvae to numerous predators, including carabid beetles. Significantly more carabid beetles are found in uncut residual strips than in clearcut strips or dense stands.[4]

Ants

Our knowledge of ants preying on small larvae of the spruce budworm is limited. Most observations concern predation on large larvae, pupae, and adults of the budworm. However, Varty and Titus (1974) included ants among the arthropods that prey on the small-larval instars. The authors concluded that predatory arthropods exercised a light restraint on budworm abundance in the egg and small-larval stages.

Although not fully studied and quantified, young spruce budworm larvae are susceptible to ant predation during the first- and second-instar dispersal periods. Numerous larvae are lost during both dispersals (Morris and Mott 1963). They spin down from host-tree crowns and alight on intervening surfaces, including nonhost vegetation and the forest floor. During these active, mobile periods, the larvae are exposed to numerous predators, including ants.

[4]Jennings, Daniel T.; Houseweart, Mark W.; Dunn, Gary A. Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce–fir forests of Maine. [Unpublished manuscript]

Finnegan (1978) noted that because young larvae are concealed in foliage, predation by the introduced red wood ant, *Formica lugubris* Zett., had been light on the first three instars of the spruce budworm. Apparently these observations were made after larval dispersal, when the young larvae had established feeding sites in old needles and new, expanding buds.

In northern Maine, ants generally were active during most of the budworm's developmental stages.[3] For both study years, ants were especially active during dispersal of the first instars in July. Strip clearcutting increases nonhost vegetation and contributes to dispersal losses of these early-stage larvae (Jennings et al. 1983) by exposing the larvae to ants.

Additional studies are needed to evaluate the importance of ants as predators of small larvae of the spruce budworm. Finnegan (1974) noted that the period of ant activity was long in Quebec, extending from mid-April to mid-October. This period spans both dispersal periods of the early instars. No doubt, ants prey on first instars before the larvae spin hibernacula for overwintering, and again the following spring before the second instars establish feeding sites. Because both predator and prey are small, special techniques are needed for study and evaluation.

Miscellaneous Insects

Dowden et al. (1950) noted that C. F. Speer discovered two predaceous insects that feed externally on budworm larvae in their hibernacula. They refer to a few *Tetrastichus* sp. (Hymenoptera: Eupelmidae) and several cecidomyid individuals (species undetermined) feeding on larvae placed on small balsam fir trees. Cecidomyids are gall midges or gall gnats (Diptera: Cecidomyiidae). Larvae of about two-thirds of the more than 1,200 North American species cause galls on plants (Borror et al. 1976); and a few species are predaceous on aphids, scale insects, and other small insects. Varty (1977) reported that the cecidomyiid larva *Lestodiplosis* sp. is a predator of small insects, including small spruce budworms and aphids.

Undoubtedly there are many other predaceous insects that feed on small larvae of the spruce budworm. Predators of overwintering larvae (Miller 1958) and of dispersing larvae have received little attention (Mott 1963).

Birds

Small larvae of the spruce budworm generally are not considered important food for birds. Cheshire (1959) reported that birds do not feed on small larvae. However, Miller (1958) included predation by chickadees and nuthatches among the possible factors responsible for losses of overwintering larvae in hibernacula. Such predation destroys all trace of the hibernaculum.

Predators of Large Larvae

Early-instar larvae are susceptible to predation during both larval dispersal periods, i.e., in the summer after egg hatch (when the first instars seek overwintering sites) and again in the following spring (when second instars seek feeding sites). Mott (1963) indicated that predation during these dispersals probably was due to spiders and predaceous insects, not birds. Kendeigh (1947) considered budworm larvae as important food items for birds only after the larvae reached an appreciable size (about one-quarter to one-half inch [0.6 to 1.3 cm]). Morris et al. (1958) also indicated that the budworm does not become attractive to most species of birds until the fourth instar is reached.

During population dynamics studies on the Green River Watershed, New Brunswick, data were collected on bird consumption of spruce budworms (Mook 1963). Of the total budworms eaten, fewer than 1 percent were in the fourth instar or smaller.

In Maine, we collected two female downy woodpeckers, *Picoides pubescens* (L.), and one black-capped chickadee, *Parus atricapillus* L., (sex undetermined) in mid-March before second instars emerged from hibernacula. However, none of these birds had fed on spruce budworms.

Predators of large larvae (L_4–L_6) of the spruce budworm include spiders, dragonflies, beetles, spruce coneworms, ants, wasps, fish, mammals, and birds.

Spiders

Large larvae of the spruce budworm are susceptible to predation by spiders (Arachnida: Araneae). Larvae fall prey to both foliage-searching and web-spinning spiders. Most predation on large larvae probably occurs when the larvae leave their feeding shelters in search of food. In reference to dropping larvae of the western spruce budworm, Turnbull (1956) noted that larvae sometimes were intercepted by spider webbing. An ensnared larva usually is subdued quickly by the host spider.

Watt (1963) estimated about a threefold increase in spider density as the spruce budworm increased from 2 to 180 larvae per 10 ft² (1.9 to 168/m²) of foliage during the 1949 to 1959 budworm outbreak on the Green River Watershed in New Brunswick. Despite these increases, he concluded that spiders and other insects show essentially no numerical response to budworm numbers. He estimated that a thirtyfold increase in attack rate of individual predators would be required to suppress population growth of the spruce budworm. However, at low larval densities, only 0.46 larva per 10 ft² (0.42/m²) of foliage would have to be eaten by predators to account for a decrease in budworm survival rates.

Loughton et al. (1963) noted a functional response of spiders to fluctuations in budworm populations on the Green River Watershed in New Brunswick. Using serological techniques, they estimated that 20 percent of the foliage-collected spiders gave positive tests when the budworm population was high; only 8 percent gave positive tests when the population was significantly lower. During late June to mid-July, when sixth instars were present, 21 and 26 percent of the spiders tested gave positive results. Antigens of large larvae were detectable for longer periods than antigens of small larvae, i.e., regularly for 4 or 5 days and commonly for 6 days. Laboratory feeding rates indicated that on average most spiders will feed on a fourth-instar budworm every third day.

On the basis of percentages of field-collected spiders giving positive serological tests, Loughton et al. (1963) concluded that species of Theridiidae were the most effective predators. Both adult and immature theridiids can attack and successfully subdue large larvae of the spruce budworm. In Maine, we have observed *Theridion pictum* (Walckenaer) preying on late-instar spruce budworms. Jumping spiders (Family Salticidae) also can attack large larvae. Loughton et al. (1963) concluded that the Salticidae should be considered important predators of the budworm at all stages of larval development.

Additional studies are needed to determine the important species of spiders preying on large larvae of the spruce budworm in spruce–fir forests. Because of their abundance, diversity, and predatory capabilities, they are undoubtedly important agents of budworm mortality. Renault and Miller (1972) concluded that spiders might play a significant role in determining endemic densities of budworm populations between outbreaks but have little influence in regulating explosive outbreaks.

Dragonflies

Dragonflies (Insecta: Odonata) are voracious predators. Both the aquatic nymphs and the terrestrial adults feed on a variety of prey, chiefly insects. Most species are commonly associated with aquatic habitats; however, many are found in terrestrial habitats, including spruce–fir forests. Adult dragonflies often patrol territories along forest roads and trails, where they "hawk" flying insects.

The prey of adult Odonata include several different orders of insects. Clausen (1940) found that Diptera, Lepidoptera, and Hymenoptera constituted the bulk of the prey. Bell and Whitcomb (1961) reviewed the literature for dragonflies preying on Lepidoptera.

Apparently only one observation has been made of dragonflies feeding on larvae of the spruce budworm. Liscombe and Lejeune (1949)

reported that dragonflies (species undetermined) were predators of spruce budworm larvae in the Spruce Woods Forest Reserve of Manitoba. In 1948 they observed "hordes" of dragonflies preying on spruce budworm larvae and concluded that dragonflies were responsible for much of the unknown mortality to spruce budworm. Unfortunately, the manner of predation was not described—we do not know if the dragonflies captured dropping budworm larvae or actively picked the larvae from foliage.

In Maine we have observed dragonflies patrolling and hawking spruce budworm moths near tree crowns, but we have not observed them capturing budworm larvae. Because mortality factors operating during the late-larval stage often influence generation survival (Watt 1963), additional observations of these predators of large larvae are needed.

Beetles

Most of our knowledge about beetle predators of large budworm larvae concerns the carabids or ground beetles (Coleoptera: Carabidae) and the coccinellids or ladybeetles (Coleoptera: Coccinellidae). Other beetle families also contain predaceous species, but little is known about their feeding habits in northeastern spruce–fir forests.

Carabid beetles are among the dominant predatory arthropods in many terrestrial communities. Their abundance in northeastern spruce–fir forests infested with the spruce budworm has been documented by Varty and Carter (1974) in New Brunswick, by Freitag et al. (1969) and Freitag and Poulter (1970) in Ontario, by Krall (1977) and Jennings and others[4] in Maine, and by Reeves et al. (1983) in New Hampshire. Although many species are arboreal, most studies concern the ground-inhabiting fauna.

Carabid beetles are chiefly opportunistic predators. Some species are both predatory and phytophagous; others are strictly phytophagous (Lindroth 1969, Johnson and Cameron 1969, Kulman 1974). Predaceous species feed chiefly on other insects, including large larvae of the spruce budworm.

Using radioactive tagging techniques, Krall (1977) identified the following nine species that had fed directly on spruce budworm larvae or secondarily on other predators of spruce budworm larvae: *Pterostichus adstrictus* Eschz., *P. coracinus* (Newm.), *P. adoxus* (Say), *P. rostratus* (Newm.), *P. scrutator* Lec., *P. pensylvanicus* Lec., *Synuchus impunctatus* (Say), *Calathus ingratus* Dej., and *Sphaeroderus canadensis* Chd. In all, 133 beetles were radioactive, or 16 percent of the 824 carabid beetles collected in pitfall traps. The authors concluded that vulnerability of spruce budworm larvae to predation by carabid beetles is extremely great once the larvae are on the ground. Of

the nine radioactive species, *P. adstrictus* apparently was the most important predator of spruce budworm larvae, with 24 and 23 percent of the total beetles of that species radioactive in insecticide-treated and control plots, respectively (Krall 1977).

Sanders and van Frankenhuyzen (1979) observed *Calosoma frigidum* Kirby eating late instars of the spruce budworm in two white spruce plantations near Sault Ste. Marie, ON. These beetles are also predaceous on the forest tent caterpillar, *Malacosoma disstria* Hübner, and the saddled prominent, *Heterocampa guttivitta* (Walker). More beetles were seen on fully foliated trees than on trees without foliage or with only peripheral foliage. The observers estimated that as many as 40 beetles may inhabit a 49-ft (15-m) spruce. The authors concluded that these beetles may have played an important role in reducing budworm populations in spruce plantations because of their size, numbers, and manner of searching current foliage (fig. 5).

On the basis of five criteria—number of individuals, habitat preference, seasonal activity, size, and food habit—Reeves et al. (1983) identified eight species of carabid beetles that are potentially important predators of the spruce budworm in northern New Hampshire. However, based solely on seasonal activity, species that are potential late-larval feeders on spruce budworm were *P. pensylvanicus* Lec., *Platynus decentis* Say, *Calosoma frigidum* Kirby, *S. canadensis* Chd., *S. lecontei* Dej., *Harpalus herbivagus* Say, and *H. pleuriticus* Kirby. Both *P. pensylvanicus* and *P. decentis* were abundant in mid- and late June, when large larvae of the budworm were present. Species with population peaks in mid-June were *S. lecontei*, *S. canadensis*, and *C. frigidum*.

Although synchrony of predator–prey activities is important, food habits and feeding preferences also must be considered. For example, both *H. herbivagus* and *H. pleuriticus* are herbivorous; *S. canadensis* and *S. lecontei* are snail feeders (Reeves et al. 1983). Thus, the list of potentially important predators of late-instar budworms narrows to three species: *P. pensylvanicus*, *P. decentis*, and *C. frigidum*. Future studies should concentrate on these species, particularly *C. frigidum*, which is a well-known predator of lepidopterous larvae (Gidaspow 1959). To our knowledge, *C. sycophanta* L., an exotic species introduced to combat the gypsy moth in New England, has not been observed feeding on the spruce budworm.

In northern Maine, 13 genera and 23 species of carabid beetles were collected by pitfall trapping in a budworm-infested forest.[4] Of the species caught, *P. adstrictus* and *P. decentis*, both potential predators of spruce budworm, were the most abundant. For both study years, seasonal activity of carabid beetles was greatest during the early- and late-larval stages of the spruce bud-

Figure 5—Ground beetle, *Calosoma frigidum*, with spruce budworm larva.

worm. Activity generally declined after budworm pupation and moth flight. *C. frigidum*, a known predator of budworm larvae, was collected in residual stands of strip clearcuts and in dense stands but not in clearcut strips. Apparently this carabid beetle prefers habitats with little ground cover or with abundant humidity (Kulman 1974).

Coccinellids or ladybeetles are predaceous on large larvae of the spruce budworm. Coccinellid larvae (species undetermined) were included among the known predators of spruce budworm larvae during investigations of the budworm's population dynamics on the Green River Watershed, New Brunswick (Dominion Department of Agriculture 1950). Smith (1966) collected individuals of *Anatis mali* (Say) that had fed on larvae of the spruce budworm. Collections of this species were made in June from fir and spruce in Ontario, presumably during the late-larval stage of the budworm.

In Maine, larvae of *A. mali* were observed from early June to mid-July in synchrony with the late-larval stages of the spruce budworm.[2] Although late instars of the predator are more voracious than earlier instars, the extent of predation on budworm larvae is unknown.

Interestingly, populations of coccinellid beetles were invariably found at higher densities in areas sprayed for spruce budworm suppression than in unsprayed areas of New Brunswick (MacDonald and Webb 1963). Populations of other predaceous insects declined immediately following insecticide treatment. The reasons for these apparent differential effects are not known; presumably, some natural enemies of coccinellid beetles were affected by insecticidal spraying.

Predation by staphylinid beetles (Coleoptera: Staphylinidae) on spruce budworm larvae apparently has not been observed; however, these beetles are abundant in northeastern spruce–fir forests. Most species of staphylinid or rove beetles are predaceous, and the larvae usually are found in the same habitats as the adults (Borror et al. 1976). Undoubtedly larvae of the spruce budworm are susceptible to predation by staphylinid beetles, but the budworm's active, often secretive habits make direct observations of predation difficult.

Spruce Coneworms

Larvae of the spruce coneworm, *Dioryctria reniculelloides* Mutuura and Munroe (Lepidoptera: Pyralidae), are predaceous on large larvae of the spruce budworm. The spruce coneworm, also called "spruce foliage worm" and the "spruce needleworm," previously was known as *D. reniculella* Grote. Coneworm larvae feed on both foliage and cones of spruces. Their habits were described by McKay (1943) and more recently by McLeod and Daviault (1963).

In a mixed infestation of both spruce budworm and "spruce foliage worm" in the Spruce Woods Forest Reserve, Manitoba, Barker and Fyfe (1947) observed that considerable mortality was inflicted on budworm larvae by larvae of the foliage worm. However, predation took place only when an insufficient supply of spruce foliage was available to larvae of the foliage worm. In a campsite experiment, equal numbers of budworm and foliage worm larvae were placed in separate containers with varying amounts of spruce foliage. Predation by the foliage worm was observed only in jars without foliage or with a scant supply, but not in jars containing an adequate supply of foliage. After 9 days of extreme food shortage and starvation, the only surviving larvae were foliage worms.

From 1946 to 1949, the annual drop in spruce budworm populations in the Spruce Woods Forest Reserve ranged from 86 to 97 percent (Liscombe and Lejeune 1949). Most of this mortality occurred between the time of early-larval emergence and the pupal period. The authors concluded that predation probably accounted for much of the mortality. They reported that the "spruce foliage worm" and dragonflies were the most important predators of the spruce budworm.

Spruce coneworms not only prey on larvae of the spruce budworm but also compete for food and shelter (Liscombe and Lejeune 1949). Relative abundances of both species are possible indicators of predator pressure, i.e., when populations of spruce coneworms increase, populations of spruce budworm decrease correspondingly (Liscombe and Lejeune 1949, Warren 1954). Warren (1954) also showed that foliage age influences predation. In a replicated laboratory experiment, many more larvae of the spruce budworm were destroyed when only old foliage was provided than in the presence of new foliage.

MacKay (1943) noted that the spruce foliage worm was predaceous on jack pine budworm in northeastern Ontario. McLeod and Daviault (1963) summarized records of *D. reniculella* feeding on the spruce budworm and also noted that the young larvae are occasional predators of a spruce needle miner, *Eucordylea piceaella* (Kerfott) (now known as *Coleotechnites piceaella* [Kerfott]).

Ants

Ants have long been recognized as potential biological control agents of forest pests. They have been studied for more than 60 years in Europe, where elaborate techniques have been developed for collecting, rearing, and propagating ants used in forest-pest control (Finnegan 1971). Only within the past 20 to 30 years has much attention been devoted to the prospects of using ants to control forest pests in North America.

Finnegan (1974) listed several qualities possessed by predaceous red wood ants, which are not commonly

found among other predators of forest pests:

1. They can attain very high population densities. Red wood ants are not host dependent but change their diet according to available prey.

2. Their foraging area or hunting ground covers all levels of the forest from the forest floor to the uppermost branches of tree crowns.

3. Their period of activity is very long, about 180 days in Quebec. Activity begins near the nest before the last snow melts in the spring and continues until the ground starts to freeze in the fall. Activity generally is continuous—24 hours a day—though reduced at night.

4. The more desirable species are polygynous, i.e., there are many queens per nest. This feature assures a long life to the nest because old queens are replaced continuously.

5. Desirable species form colonial nests, i.e., the nests are not isolated socially from neighboring nests. This creates stability and permanence in the ant population over large areas.

6. Red wood ants do not limit their predation to particular prey life stage: they may attack eggs, larvae, pupae, cocoons, or adults with equal vigor.

7. Hunting activity is regulated by the nest: individual ants hunt for the queens, their brood, and other workers, not strictly for themselves.

8. As prey populations increase, ants specialize in hunting the most abundant prey, i.e., functional responses to increasing prey densities.

Ants are among the most important predators of large larvae of the spruce budworm. Records of ants preying on various *Choristoneura* species, including *C. fumiferana*, were summarized earlier (Jennings 1971). One early record (Dominion Department of Agriculture 1950) should be added; ants (species undetermined) were observed carrying larvae of the spruce budworm from a canvas mat in the Green River Watershed, New Brunswick. More recently, Finnegan (1978) and McNeil et al. (1978) have shown that the introduced red wood ant is an effective predator of the spruce budworm in Quebec. Lab tests showed that this species was highly aggressive in searching for and attacking fourth, fifth, and sixth instars of the spruce budworm. After importation, release, and establishment of colonies, the seasonal predatory activity was observed; more than 95 percent of the prey were insects. Lepidoptera were the major prey during two peaks of predation, and fully 80 percent of the tortricid prey were spruce budworms. At peak predation, an estimated 5,298 larvae were brought to the nest per day. During the 20-day period that large spruce budworm larvae were available, an estimated 43,500 larvae were consumed per nest (McNeil et al. 1978).

The impact of this predation by red wood ants also was measured in terms of defoliation. Finnegan (1977) estimated defoliation in 1974 and 1975 at 30.0 and 42.8 percent where ants were present; this compares with

42.5 and 63.1 percent in neighboring areas without red wood ants.

Finnegan (1978) concluded that red wood ants can be an important control factor at endemic population levels or during the initial phase of a developing outbreak. McNeil et al. (1978) believed that the species could play a role in an integrated control program against the spruce budworm. Similarly, Campbell and Torgersen (1982) concluded that native predaceous ants may play an important role in the population dynamics of the western spruce budworm in Washington.

Ants certainly deserve more attention and study, particularly in the northeastern United States and Canada. Although Finnegan (1971) concluded that none of the native species showed promise as limiting agents of forest pests in Quebec, he did indicate that some species of *Camponotus* and *Formica* showed several desirable qualities. A species of *Camponotus*, *C. herculeanus* (L.), is one of the most abundant ants in strip clearcut and dense spruce–fir stands of northern Maine.[3] Further studies are needed to determine its predatory impact on large larvae of the spruce budworm.

Wasps

Wasps (Insecta: Hymenoptera) are beneficial insects. Many are parasites, others are predators of various insect pests, and some are pollinators. Most predaceous wasps belong to the Superfamily Vespoidea, which includes the familiar yellowjackets, hornets, paper wasps, and potter wasps. Some vespoids are social and build large papery nests, where the queen wasp and workers rear numerous young. Other vespoids are solitary: after mating, the adult female wasp constructs a nest in the ground or in some natural cavity and then provisions cells of the nest with food for her offspring. Adult vespoid wasps generally feed on sap or nectar, but their larvae are fed insect prey.

Yellowjackets and hornets (Hymenoptera: Vespidae: Vespinae) along with paper wasps (Hymenoptera: Vespidae: Polistinae) often are considered pests because they sometimes interfere with man's activities, and they possess a sting that may cause a serious allergic reaction. However, these wasps are beneficial insects that prey on numerous insect pests. The beneficial aspects of these wasps remain largely unreported. Akre et al. (1980) noted that researchers frequently have observed yellowjackets preying on defoliators in forests, but little has been published about this predation and its possible values.

We found no published information on vespoid wasps preying on large larvae of the spruce budworm; however, we suspect that such predation may be common. During population dynamics studies on the Green River Watershed, New Brunswick, efforts were made to collect all

winged insects that visited four balsam fir trees infested with spruce budworm (Morris 1963). Only two predatory wasps were collected during the 2-hour examination periods, and the investigators tentatively concluded that winged insect predators were of minor significance compared with spiders. But other observers (D. Mullen, personal communication) have witnessed "swarms" of hornets on infested fir and spruce trees, apparently searching for and feeding on late instars of the spruce budworm.

Most of our knowledge about predaceous wasps preying on large larvae of the spruce budworm concerns the potter or eumenid wasps (Hymenoptera: Eumenidae). These solitary wasps also are known as trap-nesting wasps because they will accept and provision artificial nests constructed from blocks of wood with predrilled borings. Eumenid wasps nest in natural cavities of stems, branches, and stumps (Krombein 1967), or in small holes bored in blocks of wood. The foundress female wasps construct mud-partitioned cells in these nests, and the cells are provisioned with paralyzed lepidopterous larvae. The paralyzed prey larvae serve as food for the developing wasp larvae.

Apparently Fye (1962) was the first to observe and report on eumenid wasps preying on late instars of the spruce budworm. He identified three species—*Ancistrocerus catskill albophaleratus* (Saussure), *A. tigris tigris* (Saussure) (= *A. adiabatus adiabatus* [Saussure]), and *Rygchium leucomelas* (Saussure) (= *Euodynerus leucomelas* [Saussure])—whose nesting activities coincided with late instars of the spruce budworm and associated spruce–fir defoliator complex in the Black Sturgeon Lake region, Ontario. Provisions of the first generation of these wasps, particularly *E. leucomelas*, included the spruce budworm (fig. 6) and the jack pine budworm. He concluded that solitary wasps may satisfactorily sample endemic numbers of important prey species, particularly the spruce budworm. Thus, the trap-nesting technique may be a useful tool for early detection of endemic budworm populations.

Larvae of the spruce budworm also were included in the diverse prey of *R. leucomelas* (= *E. leucomelas* [Saussure]) and *A. catskill albophaleratus* (Saussure) found in provisioned nests placed in the Black Sturgeon Lake region, Ontario (Fye 1965a). Individual cell data indicated that hunting female wasps tend to prey on a given species of tree or plant at one time. For example, not only were larvae of the spruce budworm taken but also larvae of other defoliator species of white spruce. Because of this consistency in searching habit, Fye (1965) concluded that it may be possible to use the wasp's superior searching ability as a technique for sampling populations of particular prey species.

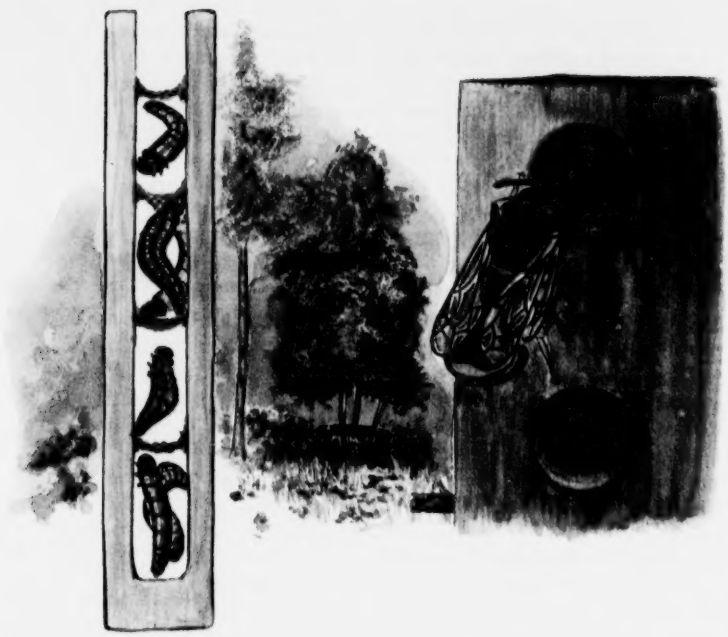

Figure 6—Trap-nesting wasp with spruce budworm larval prey provisioned in nest.

Krombein et al. (1979) also listed *C. fumiferana* as prey of *E. leucomelas leucomelas* (Saussure) and *A. catskill albophaleratus*.

In northern Maine, Jennings and Houseweart (1984) found four species of eumenids—*Ancistrocerus adiabatus* (Saussure), *A. antilope* (Panzer), *A. catskill* (Saussure), and *Euodynerus leucomelas* (Saussure)—that accepted and provisioned trap-nesting blocks placed in a spruce–fir forest. The wasps clearly preferred the more open habitats of strip clearcuts, which had abundant floral forage, to dense spruce–fir stands. Two species, *A. catskill* and *E. leucomelas*, preyed on late instars of the spruce budworm and on other lepidopterous defoliators

of northeastern hardwoods and softwoods. Spruce budworm larvae accounted for 38 percent of the total prey observed in 1977 but only 3 percent of the total prey observed in 1978. Apparently the wasps switched to a more preferred or locally abundant prey the second year.

Fish

Because of habitat differences, fish are not strictly predators of spruce budworm. However, larvae dropping into forest streams are susceptible to predation or scavenging by fish. Larval droppage may be natural or induced by spraying of chemical insecticides (Hydorn et al. 1979), and feeding on larvae spinning out of streamside trees may be intense. Kingsbury and Kreutzweiser (1980) found an average of 26.8 spruce budworm larvae in a sample of 10 brook trout, *Salvelinus fontinalis* (Mitchell), collected from a stream in Temiscouata County, Quebec, on June 14, 1978. Budworm larvae contributed over 60 percent of the volume of food items in the trout stomachs. Once the larvae fall into the water, they are essentially lost to the population, regardless of predator activity.

As a source of predator-induced mortality, predation by fish is indirect and secondary to other more important sources of budworm mortality. However, the predatory activities of fish should be considered in evaluating the environmental impacts of insecticides on nontarget organisms.

Mammals

Although mammals may reach greater population densities than birds, little attention has been devoted to determining the species of mammals preying on spruce budworms. Morris (1963) indicated that the budworm was available to purely terrestrial mammals only when populations were high, resulting in foliage depletion and larvae dropping from host trees. Some mammals, however, are arboreal. C. H. Buckner trapped specimens of the deer mouse *Peromyscus maniculatus abietorum* Bangs without difficulty in the crowns of mature balsam fir trees on the Green River Watershed, New Brunswick (Morris 1963). It was not known whether *Peromyscus* had discovered an abundant supply of budworm larvae in the crowns or their presence was due to normal foraging activity.

Earlier Morris et al. (1958) examined possible numerical responses of small mammals to changing populations of spruce budworm on the Green River Watershed. They found only two species that showed direct but weak responses: the short-tailed shrew, *Blarina brevicauda* (Say); and the rock vole, *Microtis chrotorrhinus* (Miller). Interestingly, both the deer mouse *P. maniculatus* (Wagner) and the red-backed vole, *Clethrionomys gapperi* (Vigors), showed possible inverse responses to increasing budworm populations. The authors attributed these declines in mammal populations to indirect causes, i.e.,

severe defoliation and tree mortality reduced the supply of balsam fir seed, which is the rodent's main source of winter food.

Otvos (1981) reported that three small mammals may feed on the spruce budworm in Newfoundland: the meadow vole, *M. pennsylvanicus* (Ord); the masked shrew, *Sorex cinereus* Kerr; and the red squirrel, *Tamiasciurus hudsonicus* (Erxleben). He noted that the first two species probably feed only on larvae that have dropped from severely defoliated trees, whereas the squirrel also may feed on budworms in tree crowns.

Red squirrels were implicated as possibly causing substantial reductions in budworm populations in northern Maine (Dowden et al. 1953). Stomach-content analyses of 24 red squirrels collected in a budworm-infested forest showed that spruce budworms accounted for 51 percent of their total food. The remainder consisted mainly of spruce coneworms, another defoliator of spruces. The investigators estimated that a single red squirrel (fig. 7) could eat 400 to 500 larvae per day.

In New Brunswick, W. F. Cheshire observed red squirrels (*T. hudsonicus gymnicus* [Bangs]) in captivity and estimated a mean food capacity of 600 to 700 mature budworm larvae or pupae per day (Morris 1963). Counts of red squirrels on some plots in the Green River Watershed indicated a population density of about 0.4 squirrel per acre (1/ha).

In western Maine and northern New Hampshire, we found evidence that red squirrels prey on endemic populations of the spruce budworm. Stomach-content analyses of 31 specimens showed that only 2 had eaten spruce budworms.

Because of their attack potential, selected rodents, particularly the red squirrel, and insectivores merit further investigation as predators of spruce budworm.

Birds

Birds are the best known and probably the most important predators of large larvae of the spruce budworm. They rival ants, spiders, carabid beetles, and predaceous wasps as budworm predators. More is known about birds preying on spruce budworms than any other predatory group.

During spruce budworm outbreaks, many species of birds prey on the abundant larvae (Mitchell 1952, Dowden et al. 1953). However, birds can consume only about 2 percent of an epidemic population (Crawford et al. 1983). Fewer species of birds prey on endemic populations, but their influence in limiting the number of larvae can be significant. Crawford et al. (1983) presented information on birds preying on spruce budworms in forest stands supporting endemic, transitional, and epidemic populations

Figure 7—Red squirrel, *Tamiasciurus hudsonicus*, preying on spruce budworm larva.

of the spruce budworm. The most important bird predators were those that maintained high population densities and high feeding rates over the lower ranges of the insect's density, and those that responded to initial rises in endemic populations. Black-capped chickadees; red-breasted nuthatches, *Sitta canadensis* L.; white-throated sparrows, *Zonotrichia albicollis* (Gmelin) (fig. 8); blackburnian warblers, *Dendroica fusca* (Müller); Nashville warblers, *Vermivora ruficapilla* (Wilson); and golden-crowned kinglets, *Regulus satrapa* Lichtenstein, were among those considered the most important predators of large larvae in northeastern spruce–fir forests.

Other important predators of large budworm larvae (fifth and sixth

Figure 8—White-throated sparrow with spruce budworm larva.

instars) are the solitary vireo, *Vireo solitarius* (Wilson); Swainson's thrush, *Catharus ustulatus* (Nuttall); black-throated green warbler, *D. virens* (Gmelin); yellow-rumped warbler, *D. coronata* (L.); Cape May warbler, *D. tigrina* (Gmelin); bay-breasted warbler, *D. castanea* (Wilson); magnolia warbler, *D. magnolia* (Wilson); and Tennessee warbler, *Vermivora peregrina* (Wilson). The Tennessee, blackburnian, and bay-breasted warblers have shown direct numerical responses to increasing budworm densities (Morris et al. 1958, Mook 1963). Inverse responses have been noted for the yellow-rumped and black-throated green warblers (Morris et al. 1958), but Gage and Miller (1978) found both of these warblers to be more abundant under outbreak than under postoutbreak conditions.

Earlier we reviewed the relationships between birds and the spruce budworm (Crawford and Jennings 1982), including predation and bird populations, methods of determining consumption of budworms by birds, life histories of important predaceous birds, and predator–prey models. Although considerable information is available on birds and spruce budworms, additional studies are needed, particularly at the endemic and transitional population levels. Such studies will help determine which species of birds are most beneficial in keeping budworm populations in check. The forest can then be managed to conserve and enhance populations of important insectivorous birds.

Known predators of spruce budworm pupae include spiders, beetles, spruce coneworms, budworm larvae, syrphids, mammals, and birds.

Spiders

Tothill (1923) estimated that of the progeny developing from each pair of spruce budworm moths laying 150 eggs, one pupa (1 percent) would be eaten by spiders. The spiders were not identified, but they probably represent hunting spiders rather than web spinners. Because pupae of the spruce budworm are relatively immobile, they are susceptible mainly to foliage-searching predators. However, spider predation as a source of pupal mortality probably is insignificant.

Beetles

Predaceous beetles attack and feed on pupae of the spruce budworm. In the Uxbridge Forest, Ontario, Thomson (1957) found adult Elateridae and Coccinellidae (species undetermined) feeding on budworm pupae. Of the 400 pupal sites examined before moth emergence, 73 were attacked by predators; however, beetles accounted for only 2.2 percent of this predation.

In spruce–fir stands of northern New Hampshire, Reeves et al. (1983) identified several species of carabid beetles that are potential predators of budworm pupae. Five criteria were used to denote potential predators, including synchrony of the beetle's seasonal activity with the budworm's

pupal stage. Five species were indicated as possible predators of budworm pupae based on seasonal activity: *Notiophilus aeneus* Hbst., *Pterostichus adoxus* (Say), *P. coracinus* (Newm.), *Calathus ingratus* Dej., and *Cymindis cribricollis* Dej. Individuals of *Agonum retractum* (Lec.), *P. melanarius* Ill., and *Synuchus impunctatus* (Say) also were abundant during the budworm's pupal period.

In spruce–fir stands of northern Maine, carabid beetle activity was greatest during the early and late larval stages of the spruce budworm; but many species were also active during late June and early July, when budworm pupation occurs.[4] Many of the same species, identified as potential budworm predators in New Hampshire (Reeves et al. 1983), also were collected in northern Maine.

Spruce Coneworms

Pupae of the spruce budworm are subject to predation by larvae of the spruce coneworm. The spruce coneworm pupates a few days later than the budworm (McLeod and Daviault 1963), and this asynchrony in life cycles makes the budworm susceptible to predation by coneworms. The coneworm occasionally is abundant, often in conjunction with epidemics of the spruce budworm (Rose and Lindquist 1977). These two rival species not only compete for food and shelter, but the coneworm preys on the spruce budworm when new foliage becomes scarce.

During predation, the coneworm spins a loose, silken cocoon that partly encloses the budworm pupa (fig. 9). Barker and Fyfe (1947) noted that as many as four pupae were eaten by the same coneworm on spruce terminals in the Spruce Woods Forest Reserve, Manitoba. Liscombe and Lejeune (1949) attributed much of the budworm's mortality in the Spruce Woods Forest Reserve to predation by coneworms; they noted that coneworms destroy both larvae and pupae of the budworm, but mainly pupae.

In a laboratory experiment, Warren (1954) found that predation of budworm pupae was much higher than that of larvae, probably because of the pupa's inability to escape the predaceous coneworm larva. In the field, as many as five budworm pupae were found in a single coneworm's larval web (Warren 1954).

In 1949, the budworm population dropped to low levels on the Spruce Woods Forest Reserve, Manitoba. Warren (1954) indicated that this drop may have been due to heavy predation by coneworms on the budworm's pupal population. Coneworm populations reached a peak in 1948.

Thomson (1977) examined 400 pupal sites of the spruce budworm in the Uxbridge Forest, Ontario. The examination was done 3 days before adult flight began. The spruce coneworm was the most abundant pupal predator and accounted for 5.8 percent of the 73 pupae attacked by

Figure 9—Spruce coneworm, *Dioryctria reniculelloides*, preying on pupa of the spruce budworm.

predators. He concluded that late instars of the coneworm are able to prey on the relatively defenseless spruce budworm pupae.

In Newfoundland, Otvos (1981) reported that in spruce stands where the ratio of coneworm to budworm is about 50:50, predation on budworm pupae is likely to be high.

In laboratory tests, Doganlar and Beirne (1978) observed larvae of *D. pseudotsugella* Munroe feeding on prepupae and pupae of the western spruce budworm. Consumption rates were one or two prey per larva per day, but when given a choice, this western coneworm preferred to feed on fresh foliage of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and attacked budworms only if such foliage was not available.

Budworm Larvae

An interesting case of cannibalism was observed in the Uxbridge Forest, Ontario, and reported by Thomson (1957). Sixth instars of the spruce budworm fed on new pupae of their own species. The pupae were less than 24 hours old and probably were susceptible because of their soft pupal cases. A microsporidian disease that retards larval development may have contributed to this cannibalistic behavior. More larvae were present than usual after the bulk of the population had pupated. Of the 400 pupal sites examined, 73 were attacked by predators; and attacks at 10 sites (2.5 percent) were attributed to budworm predation.

This source of pupal mortality is probably insignificant except perhaps under special conditions of high disease incidence.

Syrphids

Syrphid flies (Diptera: Syrphidae) resemble bees or wasps, but they lack stingers and have only one pair of wings. The larvae of syrphid flies vary considerably in habits and appearance (Borror et al. 1976). Many are predaceous.

Thomson (1957) found dipterous larvae, believed to be larvae of Syrphidae, feeding on pupae of the spruce budworm in the Uxbridge Forest, Ontario. These predaceous larvae accounted for only 0.5 percent of the total pupae attacked by predators.

Ants

As omnivorous predators, ants attack and feed on pupae of the spruce budworm. Thomson (1957) observed ants (species undetermined) feeding on pupae of the spruce budworm in Ontario. During preliminary laboratory tests with the red wood ant, Finnegan (1978) found that this species was highly aggressive in searching for and attacking late-instar larvae, pupae, and adults of the spruce budworm. The red wood ant was introduced into Quebec in 1971, and nests are now well established at Lac

Normand and Valcartier (Finnegan 1975, 1977).

The seasonal predatory activity of these introduced red wood ants was studied in 1976. Two peaks in predatory activity were noted (McNeil et al. 1978). At first the authors believed that the temporary drop between the peaks was attributable to pupation of tortricid larvae, including the spruce budworm. However, both larvae and pupae brought to the nest showed temporary reductions. The authors concluded that the reductions were due to a drop in mean daily temperature.

In northern Maine, we collected four genera and nine species of ants by pitfall trapping in a budworm-infested forest.[3] Greater numbers of *Myrmica detritinodis* Emery and *Camponotus herculeanus* (L.) were caught than other species in both strip clearcuts and in dense spruce–fir stands. Ants were active during most of the spruce budworm's developmental stages, including the pupal stage (fig. 10).

Mammals

Our knowledge of mammals preying on pupae of the spruce budworm is very limited. Potential mammalian predators of pupae include the deer mouse *P. maniculatus* (Wagner) and the red squirrel.

The deer mouse *P. maniculatus abietorum* Bangs was observed in crowns of mature fir trees on the Green River Watershed, New Brunswick (Morris 1963). There was an abundant supply of spruce budworm larvae in the tree crowns. The diet of this rodent probably includes insect pupae as well as larvae.

During the Green River studies in New Brunswick, W. F. Cheshire estimated that red squirrels had a mean food capacity of 600 to 700 mature larvae or pupae of the spruce budworm per day (Morris 1963).

In northern New Hampshire we collected red squirrels that had fed on pupae of the spruce budworm. These collections came from areas where spruce budworm populations were low. The recovery of larval–pupal remains in squirrel stomachs indicates that like birds, squirrels can search and find scarce prey.

Because budworm pupae are relatively immobile and few drop from host trees, they are not susceptible to strictly terrestrial predators, such as insectivorous shrews. Unless dislodged, most pupae remain attached by their cremaster hooks to silk spun by the larvae. Thus, mammalian predation on spruce budworm pupae is restricted largely to arboreal mammals.

Birds

Numerous birds feed on pupae of the spruce budworm; at least 49 species have been observed and recorded with pupal remains in their stomachs. Many of the same species that prey on large larvae also prey on bud-

Figure 10—Carpenter ant, *Camponotus* sp., and spruce budworm pupa.

worm pupae. Most are species of warblers, vireos, kinglets, sparrows, and grosbeaks. There are some indications that when pupae become available, fewer late-instar larvae are taken by birds (Mook 1963).

The species of birds we consider important predators of endemic-level budworm pupae in northeastern spruce–fir forests are the black-capped chickadee, red-breasted nuthatch, golden-crowned kinglet, solitary vireo, and the Nashville (fig. 11), Cape May, magnolia, yellow-rumped, black-throated green, blackburnian, and bay-breasted warblers.

During budworm epidemics, many transient birds flock into spruce–fir stands and consume large numbers of budworm pupae. These include red-winged blackbird, *Agelaius phoeniceus* (L.); common grackle, *Quiscalus quiscula* (L.); evening grosbeak, *Coccothraustes vespertinus* (Cooper); and pine grosbeak,

Figure 11—Nashville warbler searching foliage for spruce budworm pupa.

Predators of Adults

Pinicola enucleator (L.). Their feeding often is instantaneous and spectacular.

Interestingly, Johannsen (1913) reported that the purple martin, *Progne subis* (L.), fed on pupae of the spruce budworm during the 1911–12 outbreak in Maine; but the birds were only locally abundant.

In Maine and New Hampshire, we estimated that birds consumed 941 pupae per acre (2,325/ha) in stands supporting endemic populations of spruce budworm, 9,016 pupae per acre (22,279/ha) in stands supporting transitional populations, and 14,791 pupae per acre (36,551/ha) in stands supporting epidemic populations (Crawford et al. 1983). These are conservative estimates based on a pupal availability period of only 14 days.

Additional studies are needed to determine the effects of pupal predation by birds, especially at low budworm densities. Gage and Miller (1978) concluded that birds can exert a strong predation pressure on preoutbreak populations of the spruce budworm. To fully understand these regulatory processes, researchers need to determine the consequences of pupal predation on generation survival.

Predators of spruce budworm moths include spiders, dragonflies, beetles, robber flies, ants, and birds.

Spiders

Spruce budworm moths are susceptible to predation by both web-spinning and hunting spiders. Web-spinning species that are abundant in northeastern spruce–fir forests belong to the families Araneidae, Dictynidae, Erigonidae, Linyphiidae, and Theridiidae.

Vagrant hunting spiders of the families Clubionidae, Salticidae, Thomisidae, and Philodromidae also capture and feed on spruce budworm moths. Most of these hunters actively search conifer foliage for prey; however, the sedentary crab spiders (Family Thomisidae) wait in ambush for passing prey.

In British Columbia, Turnbull (1956) observed both web-spinning and hunting spiders feeding on moths of the western spruce budworm. During moth flight, webs of 39 argiopid (Family Araneidae) and 34 theridiid (Family Theridiidae) spiders were observed at night. Almost every web had captured a budworm moth; 85 moths were found in orb webs and 46 in theridiid webs. Turnbull also observed hunting salticid spiders capturing and feeding on gravid female moths. Sluggish, fully gravid females were especially vulnerable to attack by salticid spiders.

Our knowledge of spiders feeding on moths of spruce budworm in the northeastern United States and Canada is limited. Using serological techniques to detect predation, Loughton et al. (1963) estimated that in 1959 about 30 percent and in 1960 about 25 percent of the spiders collected and tested had fed on spruce budworm during the moth stage. The estimates were made when preceding budworm populations were high (433 egg masses per 100 ft^2 [46.6/m^2] of foliage) and lower (156 egg masses per 100 ft^2 [16.8/m^2]), respectively. However, the percentages do not necessarily refer only to moth predation because developmental stages overlapped (pupae, moths, and eggs).

In Maine we have collected the following species of web-spinning spiders with spruce budworm moths in their webs:

Family Theridiidae (Comb-footed spiders)
- *Theridion frondeum* Hentz
- *Theridion murarium* Emerton
- *Theridion pictum* (Walckenaer)

Family Linyphiidae (Sheet-web weavers)
- *Frontinella communis* (Hentz)

Family Araneidae (Orb weavers)
- *Araniella displicata* (Hentz)
- *Araneus marmoreus* Clerck
- *Cyclosa conica* (Pallas)

Family Agelenidae (Funnel-web weavers)
- *Agelenopsis utahana* (Chamberlin and Ivie)

Family Dictynidae
- *Dictyna foliaceae* (Hentz)
- *Dictyna phylax* Gertsch and Ivie

Species in Maine most commonly observed with budworm moths were *Theridion pictum* and *Frontinella communis*. Both species build their webs in young, understory spruce–fir trees, and each species builds a characteristic web. *T. pictum* constructs a tangle web of many ensnaring viscid threads (fig. 12). This theridiid spider also ties several spruce or fir needles together, forming a "turret" in which to hide. Discarded cadavers of budworm moths often are incorporated into the walls of the turret.

The linyphiid *F. communis* spins a "bowl and doily" web consisting of a cuplike bowl and a horizontal sheet spun beneath the bowl. Above the bowl the spider spins several irregular strands of silk of varying length to impede flying insects, many of which fall into the bowl. We commonly observed three or four budworm moths in webs of both species (fig 13).

Dragonflies

In Maine we frequently observed dragonflies hawking and capturing spruce budworm moths on the wing. These observations led to a study to determine the species of Odonata associated with spruce–fir forests of Maine and to determine by gut-content analysis the prey of adult Odonata, with special emphasis on

Figure 12—*Theridion pictum* in web with spruce budworm pupae and moth prey.

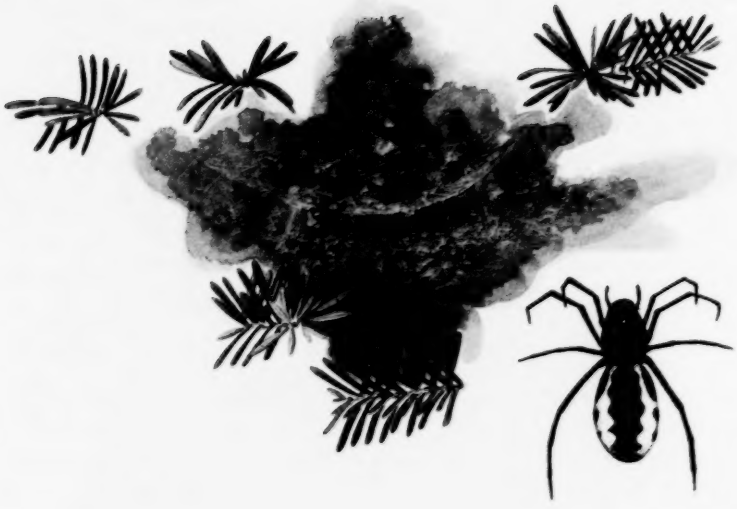

Figure 13—Bowl and doily spider, *Frontinella communis*, with spruce budworm moth prey.

identifying remains of the spruce budworm (Tsomides et al. 1982).

Odonata representing nine families, 22 genera, and 39 species were collected in spruce–fir forests of Maine. Collecting localities (14) spanned the central part of the State from the northwest to the southeast. All sites had budworm-infested trees.

Both dragonflies (suborder Anisoptera) and damselflies (suborder Zygoptera) were collected in this study (Tsomides et al. 1982). Of 350 specimens dissected and gut contents examined, 163 (47 percent) had fed on lepidopterans. Fifty percent of the Anisoptera had lepidopterous scales in their guts, whereas only 19 percent of the Zygoptera had eaten lepidopterans. The libellulids (Family Libellulidae) were the most numerous Odonata collected, representing 424 individuals. Fully 58 percent of the libellulids had fed on lepidopterans.

Although we were unable to specifically identify spruce budworm remains in the odonate gut contents, we were able to recognize lepidop-

teran scales. Comparisons of these scales with scales from laboratory-reared spruce budworms proved inconclusive. However, many of the lepidopterous scales undoubtedly were those of the spruce budworm because odonates often were collected while they were hawking budworm moths (fig. 14). One dragonfly was captured while feeding on a spruce budworm moth. Comparison of budworm moth flight information with gut-content analysis indicated that odonates were consistently feeding on moths during June and July, when spruce budworm flight occurred.

Although the results of our gut-content study are encouraging, other methods are needed to confirm this apparent widespread odonate feeding on the spruce budworm. Serological techniques offer one possible approach (McIver 1981) but may be difficult to quantify (Boreham 1979).

Beetles

Our knowledge of beetles preying on spruce budworm adults is limited and intuitive at best. Because budworm moths are highly mobile and can escape predators by flight, their susceptibility to foliage-searching beetles is limited. However, freshly emerged moths, moths in coitus, and ovipositing females may be subject to attack by beetles. Beetle predation on budworm moths is probably inconsequential.

Reeves et al. (1983) identified at least five species of carabid beetles as potential predators of spruce budworm adults. The species were *Pterostichus melanarius* Ill., *P. coracinus* (Newm.), *S. impunctatus* (Say), *Cymindis cribricollis* Dej., and *P. decentis* Say. Seasonal activities of these beetles coincided with budworm moth activity in northern New Hampshire.

In northern Maine, carabid beetles also were active during the budworm's flight period; but greatest activity, as evidenced by pitfall catches, occurred during the early- and late-larval stages of the budworm.[4]

Robber Flies

This group of dipterans (Diptera: Asilidae) contains about 850 species in North America (Borror et al. 1976), but the species found in northeastern spruce–fir forests are poorly known. Adult robber flies are found in a variety of habitats; each species usually is found in a characteristic habitat (Borror et al. 1976). The adults are predaceous and attack a variety of prey, including Lepidoptera. Prey usually is captured on the wing, and robber flies will attack insects larger than themselves.

In New Brunswick, I. W. Varty observed and collected an adult robber fly, *Asilus* sp., feeding on a spruce budworm moth. Apparently, this is the only observation of predation on spruce budworm.

Figure 14—Dragonfly hawking spruce budworm moth.

Because prey usually are captured on the wing, predation by robber flies on spruce budworm may be limited to moths. However, large larvae dropping from host trees may be eaten. The Asilidae associated with northeastern spruce–fir forests, their predatory habits, and their potential for preying on spruce budworms need to be investigated.

Ants

Few observations have been made of ants (Hymenoptera: Formicidae) preying on spruce budworm moths. Finnegan (1978) noted that *F. lugubris* attacked adults of the spruce budworm in laboratory feeding tests. Field observations of prey brought back to nests by this species included

wing fragments and abdomens, thought to be those of *C. fumiferana* adults (McNeil et al. 1978). In northern Maine, ants were very active during the adult stage of the spruce budworm, but none were observed feeding on budworm moths.[3]

We have observed ants removing and scavenging male spruce budworm moths caught in pheromone-baited traps coated with sticky materials. After capturing several moths, the trap's sticky surfaces become coated with moth scales and other debris, allowing the ants to traverse the sticky surfaces and remove the moth bodies, leaving behind only wing fragments.

Because spruce budworm moths generally are mobile and capable of flight, they are less susceptible to ant predation than earlier life stages. However, newly emerged moths, and especially egg-laden females, may be attacked by ants and other foliage-searching predators. If moths are captured before egg laying, predation on adults could be an important source of mortality.

Birds

At least 25 species of birds are known to capture and eat spruce budworm moths. Chickadees, thrushes, kinglets, vireos, warblers, grosbeaks, and sparrows are among the predators of spruce budworm moths.

We consider the following species as important predators of budworm moths in northeastern spruce–fir forests: black-capped chickadee, golden-crowned kinglet, and Cape May, yellow-rumped, and bay-breasted warblers. Most of these species have been observed hawking and capturing moths in flight.

Greenbank (1963) noted that budworm moths represented a small proportion of the gizzard content of wood warblers and flycatchers. Despite numerous hours of observation from tree platforms, he never saw birds capturing moths on the wing. Because moth populations were high in relation to bird populations, Greenbank concluded that bird predation on the Green River Watershed was probably unimportant.

The effects of moth predation by birds on population dynamics of the spruce budworm are unknown. Certainly, female moths are susceptible to predation before and during oviposition. Predation on egg-laden moths may adversely affect the succeeding generation, especially at low population densities. More observations and collections are needed during the moth stage, particularly over a range of budworm densities.

Predators As Natural Regulators

Predators are natural regulators of animal populations upon which they feed (Price 1975). Numerous mathematical models have been developed to explain the regulatory processes of predation and predator–prey interactions (Holling 1959a, 1959b, 1966; Holling and Buckingham 1976; Nicholson 1933, 1954; Royama 1971, 1977; Solomon 1949; Tinbergen 1960; Watt 1959). The spruce budworm serves as an example in some models. Predation acts as one of the most important factors in maintaining stability within ecosystems (Sailer 1971).

A predator is an organism that kills and consumes many animal-food items in its lifespan, whereas a parasite (parasitoid) requires and eats only one animal in its life (Price 1975). However, because the female parasite oviposits in numerous hosts, parasites ultimately may be responsible for killing many hosts. Sailer (1971) compared the attributes of invertebrate parasites and predators and concluded that in general, predators

- Tend to be less specific in their food habits,
- Are less dependent on a single food resource,
- Are better able to maintain stable populations that tend to exploit prey species in proportion to their relative abundance,
- Tend to be longer lived and less likely to be adversely affected by physical factors of the environment,
- Have searching capabilities that generally are greater,
- Likely have a compensatory increase in fecundity or searching capacity where food habits are specific,
- Normally contact, kill, and consume large numbers of prey organisms; by contrast, parasites spend most of their life on or in a single host.

Buckner (1971) reviewed the roles of vertebrate predators in the forest ecosystem. He advocated that forest pest control should take an integrated approach that includes the use of small vertebrates. He defined the ideal predator for encouragement as one that (1) has a high feeding capacity, (2) prefers the target insect pest, (3) selectively feeds on insects not attacked by other natural control agents (e.g., parasites), (4) maintains high population densities, (5) responds quickly to other control measures applied simultaneously, and (6) is unaffected by subsidiary treatments such as pesticides.

Predators may respond numerically and functionally (or both) to increases in prey populations. Both invertebrate and vertebrate predators can increase their reproductive potential (numerical response) in the presence of abundant food and concentrate predatory activities (functional response) on selected prey. Because many invertebrates (insects) are multivoltine (i.e., having many generations per year), they may respond sooner to prey abundances than some vertebrates. Many invertebrates and vertebrates have an acute searching capability, allowing them to find prey even at low den-

sities. Vertebrates have the added advantage of forming "search images."

Buckner (1967) stressed the importance of both numerical and functional responses of avian and mammalian predators on forest insect populations. He divided numerical responses into breeding and behavioral responses. Examples of breeding numerical responses to increasing budworm densities have been demonstrated for the Tennessee, blackburnian, and bay-breasted warblers (fig. 15) (Morris et al. 1958, Mook 1963). Behavioral numerical responses often are instantaneous and spectacular. Roving flocks of colonial nesting birds such as grackles and blackbirds that enter the forest and feed on budworms exemplify a behavioral numerical response. Such responses may be significant at high prey densities when budworms make up a large percentage of the diet (Dowden et al. 1953).

Buckner (1967) divided functional responses into basic components (reaction to increasing prey density) and subsidiary components (food preferences and feeding behaviors such as hoarding and "sport" killing). Ovenbirds, *Seiurus aurocapillus* (L.), exhibit a functional response to outbreaks of the spruce budworm by changing their feeding behavior (Zach and Falls 1975). That is, they normally restrict their feeding to or near the forest floor; but when budworms reach high densities, they search coniferous foliage and feed on larvae, pupae, and adult spruce budworms.

Populations of predators and their feeding behaviors may vary depending on densities of potential prey. Populations of the spruce budworm generally are classified as low-level or endemic populations and high-level or epidemic populations. Of course, there may be numerous gradations between these two extremes. "Outbreaks" generally refer to epidemic populations.

Endemic Spruce Budworm Populations

It is generally recognized that predators help maintain insect populations at low, endemic levels. Predators and other natural enemies such as parasites help keep potential pest populations in check until they are released, usually by some climatic factor or combination of abiotic and biotic factors. However, the importance of predators and their potential for regulating and maintaining endemic populations of the spruce budworm have not been studied in detail.

Morris (1963, p. 244) concluded that, "If predation has any important influence on the dynamics of budworm populations it must, therefore, be exerted during the endemic period, or during the early years of population release . . . ." Other investigators have reached similar conclusions regarding the importance of natural control mechanisms operating against

Figure 15—Bay-breasted warbler searching foliage for budworm larval prey.

low-level populations of the spruce budworm (Miller and Varty 1975). However, our knowledge and understanding of the specific predators and their regulatory functions during endemic populations of the spruce budworm is limited. Virtually nothing is known about invertebrate predators and endemic budworm populations. And little information is available on vertebrates and their importance in maintaining low-level populations.

Dowden et al. (1953) concluded that in light infestations of the spruce budworm, predation by birds should be of great economic importance. Gage and Miller (1978) concluded that birds can exert a strong predation pressure on preoutbreak populations of the spruce budworm. Morris et al. (1958) indicated that birds can be extremely important when budworm populations are at endemic levels of 1,000 or fewer per acre ($\leq$ 2,471/ha).

At least two studies point to the possible influence of predation on release of spruce budworm populations. Graham and Orr (1940) suggested that the 1912 outbreak of the spruce budworm in Minnesota might have been precipitated or caused by the scarcity of small insectivorous birds. Thousands of migrating warblers were killed by late snow and ice storms during the late springs of 1907 and 1910. Warbler populations had recovered to only about 10 percent of their former numbers when the budworm outbreak started in 1912. In New Brunswick, Morris (1948) noted that another defoliating insect of balsam fir, the eastern blackheaded budworm (*Acleris variana* [Fernald]), reached a high population level in the late 1940's. He suggested that these high populations of an alternate food source may have relieved predation pressure on the spruce budworm, thus aiding in population release.

In northern New Hampshire, the estimated seasonal consumption by birds exceeded 1,336 larvae and 931 pupae per acre (3,300 larvae and 2,300 pupae/ha) when budworm populations were endemic (Crawford et al. 1983). These estimates were derived by determining daily consumption rates (Gage et al. 1970) and multiplying by 20 and 14, the estimated number of days large larvae and pupae were present, respectively. These estimates represent predation by species that are adapted for and capable of finding sparsely distributed budworms. Overall, predation by birds amounted to 87.2 percent in spruce–fir stands supporting endemic populations. This is a conservative estimate because not all species of birds were sampled, some sample sizes were small, and estimates of seasonal availability were moderate, e.g., Mook (1963) estimated that sixth-instar larvae are available for 30 days.

At low larval densities of the spruce budworm, Watt (1963) estimated that only 0.46 larva per 10 ft^2 (0.42/m^2) of foliage would have to be eaten by predators to account for a decrease in survival rate. Predator populations as

low as one pair of breeding birds per acre along with one or two spiders per 10 ft^2 (0.9 to 1.9/m^2) of foliage (300,000 ft^2/acre = 30,000 to 60,000 spiders/acre; 68,869 m^2/ha = 74,130 to 143,260 spiders/ha) have considerably more feeding potential than Watt's estimated value. Additionally, we can increase bird populations with appropriate silvicultural modifications in spruce–fir stands (Crawford and Titterington 1979, Titterington et al. 1979), thus increasing predator potential.

In summary, we have very little information about predators, predation, and endemic populations of the spruce budworm. Much more work needs to be done to fully understand the regulatory roles predators play in maintaining budworm populations at low levels.

Epidemic Spruce Budworm Populations

Predators may affect budworm populations before, during, and after outbreaks. The absence or lack of predation may be instrumental in releasing budworm populations from endemic to epidemic levels (Graham and Orr 1940, Morris 1948 and 1963, Morris et al. 1958). Predators and predation have received much more attention during an epidemic than before or afterward. Graham and Orr (1940) concluded that parasites and predators play a minor role during an outbreak, but that at the end of an outbreak they effectively destroy most stragglers. They noted that when the number of budworms is reduced by starvation, the percentage of budworms destroyed by parasites and predators reaches 85 to 95 percent.

In New Brunswick, population dynamics studies showed that the numerical responses of all predators to increasing budworm density was limited (Watt 1963, Morris 1963). Spiders and predaceous insects apparently showed limited numerical responses to increases in budworm density (Watt 1963), whereas birds showed marked increases. Buckner (1971) concluded that small mammals play an insignificant role in the dynamics of budworm populations. Earlier, Morris et al. (1958) indicated that two mammals, the short-tailed shrew, *B. brevicauda* (Say), and the rock vole, *M. chrotorrhinus* (Miller), showed possible direct numerical responses to increasing budworm populations; however, they discounted these responses as being directly related to the spruce budworm.

Morris (1963) noted that most predation on spruce budworm occurs during the large-larval period. Predation during this period is especially important because it is the period that determines generation survival for the spruce budworm. Both spiders and birds kill appreciable numbers of larvae during the late-larval period of the spruce budworm.

Birds exhibit both numerical and functional responses to increasing populations of the spruce budworm.

We have reviewed the literature describing these responses (Crawford and Jennings 1982). Direct and strong numerical responses have been observed for the Tennessee, blackburnian (fig. 16), and bay-breasted warblers (Morris et al. 1958, Mook 1963). Later, Gage and Miller (1978) showed more yellow-rumped and black-throated green warblers under outbreak than postoutbreak conditions. The ovenbird exhibits a functional response to outbreaks of the spruce budworm (Zach and Falls 1975). Ovenbirds generally restrict their feeding behavior to and near the forest floor. However, once spruce budworms reach high densities, these birds frequently were observed searching branches of infested conifers and feeding on larvae, pupae, and adults.

The percentage of budworms destroyed by birds during epidemics is usually less than 10 percent; however, up to 40 percent or more of their total diet may be spruce budworms (Mitchell 1952, Dowden et al. 1953). Kendeigh (1947) estimated that birds destroyed 4.3 percent of a heavy infestation of spruce budworms in Ontario in 1945. He estimated that one breeding pair plus their nestlings could consume 16,000 larvae and pupae per acre (39,536 larvae and pupae/ha) during the period of availability. In New York, George and Mitchell (1948) calculated that the degree of control by birds was from 3.5 to 7.0 percent when infestations were 500,000 to 1,000,000 budworms per acre (1,235,500 to 2,471,000 budworms/ha). Their estimates were more than double that of Kendeigh (1947) and represent 17,000 to 70,000 budworms destroyed per acre (42,007 to 172,970/ha). During an outbreak on the Green River Watershed in New Brunswick, populations reached 8 million larvae per acre (19,768,000 larvae/ha); however, bird predation was estimated at less than 1 percent (Morris et al. 1958).

For epidemic populations in Maine, we estimated that predation by birds amounted to 2.4 percent (Crawford et al. 1983), with total seasonal consumption of more than 21,044 larvae and 14,569 pupae per acre (52,000 larvae and 36,000 pupae/ha). The percentage predation by birds was much less in stands supporting epidemic populations than in stands supporting transitional populations (23.0 percent) or in stands supporting endemic populations (87.2 percent). Daily consumption rates for individual species of birds are summarized in Crawford and Jennings (1982).

Several investigators have indicated that birds contribute to the collapse of spruce budworm outbreaks. During a "waning" outbreak in New Brunswick in 1918, Tothill (1923) estimated that birds consumed about 13 percent of the larvae. This percentage is slightly higher than that observed during epidemics. Dowden et al. (1950) noted that insectivorous birds, largely warblers, accounted for a considerable portion of the popula-

Figure 16—Blackburnian warbler searching foliage for spruce budworm larva.

tion reduction to a collapsing outbreak in the Adirondacks in 1947 and 1948. Watt (1963) indicated that birds affected larval survival at low budworm densities; Buckner (1971) interpreted this to mean that birds may be of considerable importance in cleaning up residual populations of the pest after the major outbreak has run its course. Blais and Parks (1964) indicated that residual populations of the spruce budworm were controlled through the predatory actions of grosbeaks that invaded remaining pockets of infestation after insecticide treatment.

Spiders are also abundant during epidemics of the spruce budworm. Estimates of population densities indicate that spiders far outnumber all groups of predaceous insects on coniferous foliage (Morris 1963); populations of spiders in forest stands of medium density were estimated at 75,000 per acre (185,323/ha), not including species inhabiting the ground or lower vegetation. With a population density of two or more per 10 ft^2 (1.8/m^2) of foliage and a feeding rate of one spruce budworm larva every 3 days, Morris (1963) concluded that spiders would have a very high feeding potential compared with birds. However, their capacity to regulate epidemic populations has not been demonstrated and may be hampered by limited numerical responses (Morris 1963) compared with exploding prey populations.

In summary, most of our knowledge about predators, predation, and epidemic spruce budworm populations concerns only two predator groups, birds and spiders. The impacts caused by other predator groups, both invertebrate and vertebrate, need investigation over a range of predator-prey densities.

Methods for Studying Predation

Measurement of predation in field populations is notoriously difficult (Morris 1963). Unlike parasites and diseases, predators often leave little or no evidence of their feeding activity. Many predators are cryptic and secretive; others are nocturnal, making observations difficult except with specially designed equipment.

Buckner (1966) indicated that three basic measurements must be taken to obtain a true understanding of predator–prey systems: density of prey, density of predators, and extent of destruction of prey by predators. Sampling methods generally have been worked out for each life stage of the spruce budworm (Morris 1955, Miller 1958, Sanders 1980), but methods for determining predator densities are often lacking. Estimates of prey consumption require determinations of seasonal availability, predator feeding behaviors, and the proportion of prey in the predator's total diet. Buckner (1966) discussed five factors to consider when evaluating individual predator species:
(1) food capacity of the predator,
(2) effects of alternate foods,
(3) prey defense mechanisms,
(4) numerical responses of predators to increasing prey populations, and
(5) functional responses of predators to prey populations.

Despite numerous limitations, both direct and indirect methods have evolved for studying the effects of predators on prey populations. These methods include techniques for observing predators in action, identification of predator feedings, and identification of prey remains in predator stomachs or in feces. Numerous techniques used include exclusion techniques, direct assessments, serological tests, tagging with radioisotopes, direct observations, and photographic recordings. Buckner (1966), Kiritani and Dempster (1973), DeBach et al. (1976), and Southwood (1978) reviewed pertinent literature available for assessing predation. We discuss some of the techniques applicable to spruce budworm.

Exclusion Techniques

These include (1) mechanical exclusion, (2) insecticidal check method, (3) biological check method, and (4) hand-removal techniques. Mechanical exclusion is achieved by constructing sleeve or larger cages to exclude predators (Campbell et al. 1981). Disadvantages of this technique are that dispersal of prey is prevented, the physical environment is modified by the cage (DeBach and Bartlett 1964), and predator identities usually are unknown, though some indication can be gained by varying mesh sizes, e.g., birds *vs.* ants. Both insecticidal and biological check methods employ "before and after" observations or "check-treated" observations in conjunction with an insecticide or biological used selectively to kill predators (Kiritani and Dempster 1973, DeBach et al. 1976). Hand removal of predators probably is the most reliable exclusion tehnique, but it is extremely time consuming and costly.

Direct Assessments

Direct assessments of predation include stomach-content analyses, counting corpses killed by a predator (e.g., insects in spider webs [Turnbull 1960]), examining feces or fecal pellets for prey remains, and placing known numbers of prey in the field. Stomach-content analyses require a thorough knowledge of the flora and fauna where samples are collected (Korschgen 1980), and particularly familiarization with budworm morphology of all life stages. Some predators thoroughly masticate their prey, making postmortem identifications difficult. Counting corpses also has drawbacks because some predators bury their prey. Placing prey in the field has a disadvantage in that the rate of attack may be affected by density, position, or exposure of prey (Kiritani and Dempster 1973).

Serological Tests

Serological tests offer one of the most convenient, reliable methods for assessing predation, especially by invertebrate predators. This technique has been used to determine spider and mite predation on the spruce budworm (Loughton et al. 1963). Basically, prey material is identified in the gut of a predator by its reaction with the blood serum from a mammal (usually a rabbit) that has been sensitized against the prey. The blood serum contains antibodies (antisera) that react with proteins (antigens) of the target prey to form a precipitate. There have been numerous refinements to the basic "precipitin test," and new, more sensitive tests have been developed (see Miller 1979 for a review).

Serological techniques have been used **qualitatively** to identify the predators of particular prey species, though **quantitative** estimates of predation are possible under certain conditions (Kiritani and Dempster 1973, Dempster 1960). The minimum number of prey eaten can be estimated by this equation:

$$\text{Prey eaten} = (PmT)/t$$

where P is the number of predators present, m is the proportion of those tested that gave positive serological reactions, T is the total time that prey are available for predation, and t is the length of time that a meal remains detectable by serological methods (Kiritani and Dempster 1973). The latter usually is determined under controlled conditions in the laboratory with known predator–prey feedings.

Radioisotope Tagging

Radioisotopes can be used to "tag" or mark prey and identify predators feeding on the labeled organisms. Labeling of prey usually is done by immersion, by use of sprays or gases, by introduction through food or water, or by injection (Odom and Golley 1963). Krall and Simmons (1977) used phosphorus-32 injected into tree roots of balsam fir to label

the spruce budworm and identify carabid beetles preying on budworm larvae.

Kiritani and Dempster (1973) concluded that in practice, tagging with radioisotopes was extremely difficult to quantify and use because there is considerable variation in radioactivity of individual prey; many predators consume only part of their prey; excretion of the radioisotope by a predator seems to depend on the amount of food it subsequently eats; and it is difficult to ensure that the predator obtained all of its radioactivity solely from the tagged prey, i.e., the environment may become contaminated or the isotope may be passed up the food chain to scavengers and secondary predators.

Direct Observations

Direct observations of predation probably are the most reliable method; but they are costly, time consuming, and often difficult or impossible to make. Special techniques and equipment such as blinds, telescopes, and night-viewing scopes may be required. If predation is common, the frequency of observing the predator consuming the prey may be useful (Morimoto 1960); however, predation usually is difficult to observe in arboreal habitats such as tree crowns of budworm-infested trees. Photographic recordings of predators returning to nests with food may be helpful so long as the food can be recognized and identified on film. With proper electronic equipment, permanent records can be made of birds, wasps, or ants returning to their nests with prey.

Another direct observational technique entails placing predrilled blocks of wood in the forest for trap-nesting wasps (Krombein 1967). Foundress female wasps use the blocks to make their nests, which are provisioned with paralyzed lepidopterous prey. Observations can be made of the wasps bringing prey to their nests, or the blocks can be split open, the nests and cells examined, and the prey counted directly.

In summary, each technique or method for studying predation has limitations. When possible, it is best to employ more than one technique, e.g., direct field observations of predation coupled with examination of predator-gut contents.

Conservation and Enhancement of Predators

Predators and other natural enemies of the spruce budworm can be protected, maintained, and enhanced by environmental manipulation and cultural practices. The spruce–fir forest can be managed to reduce susceptibility to budworm damage and to provide suitable habitats for natural enemies of the spruce budworm. Effective management requires a thorough knowledge and understanding of predator biologies and their habitat needs, including food, cover, and nesting sites. Examples of these requirements and provisions follow.

Habitat Requirements

Bird populations respond to land-management measures (Crawford and Titterington 1979, Crawford et al. 1981, Titterington et al. 1979) and can be increased by directed forest practices. A mature managed forest containing a mix of tree species and size classes, and with scattered openings and patches of regeneration, supports populations of birds that prey effectively on spruce budworm (Crawford et al. 1983). These findings support the thesis that environmental diversity favors the conservation of and increase in numbers of beneficial organisms (Glen 1954).

Predaceous eumenid wasps prefer open areas with abundant light penetration (Fye 1972). Wasp populations were larger and more diverse in recently disturbed than in nondisturbed forests of northwestern Ontario. In northern Maine, the eumenid wasps clearly selected the more open habitats of strip clearcuts over dense spruce–fir stands (Jennings and Houseweart 1984). Strip harvesting and other measures that produce openings in the forest favor these predators of late-instar spruce budworm larvae.

In northern New Hampshire, stands of red spruce had more carabid beetles (species and individuals) than mixed stands of spruce–fir, fir–spruce, or fir (Reeves et al. 1983). Many of these carabid beetles occupying spruce stands were determined to be potentially important predators of the spruce budworm. Thus, silvicultural techniques aimed at reducing the balsam fir component would not only decrease susceptibility of the forest to budworm damage but also promote greater densities of predaceous carabid beetles.

Similarly, strip harvesting contributes to dispersal losses of early instars of the spruce budworm (Jennings et al. 1983) and provides new habitats for many predaceous arthropods, including phalangids, ants, spiders, and carabid beetles.

Food Requirements

The availability of food, including alternate food sources, is essential for encouragement of beneficial organisms (Coppel and Mertins 1977). Most predators feed on a variety of prey organisms; few have specific, restricted diets. The availability and abundance of alternate

foods can favor and maintain populations of predators during periods when target prey are scarce.

Forests can be managed to provide a mix of species that, in turn, provide food sources for numerous herbivores. The herbivores, including defoliators of spruce–fir, provide food sources (prey) for polyphagous predators. For example, eumenid wasps prey on late instars of the spruce budworm and on a variety of other lepidopterous larvae (Fye 1962, Jennings and Houseweart 1984). Most of the prey are defoliators of northeastern hardwoods and softwoods. Managing the forest to promote species diversity can provide alternate foods for predators.

The adults of numerous parasitic insects require alternate food sources such as pollen and nectar (Syme 1966, 1975; Leius 1960). Similarly, predaceous eumenid wasps are attracted to flowering plants (Fye 1972). In northern Maine, eumenid wasps were most common in open habitats with abundant floral forage (Jennings and Houseweart 1984). Managing the forest to encourage flowering shrubs and forbs will provide alternate food sources for these predators of budworm larvae. Artificial plantings and sowings of wildflower seeds also are possibilities for increasing nectar sources of preferred species. In the Soviet Union, considerable work has been devoted to the use of nectar-bearing plants to increase the effectivness of entomophagous insects (Stern et al. 1976).

Nesting Requirements

European foresters routinely provide nest boxes to encourage birds (Bruns 1959, Franz 1961), but this technique has received minimal attention elsewhere (Coppel and Sloan 1971). Artificial structures have been used to encourage predaceous *Polistes* wasps in agroecosystems (Lawson et al. 1961, Kirkton 1971). Apparently, this technique has not been used in northeastern spruce–fir forests, where species of *Vespula* are common.

Nesting materials can be provided to attract and encourage nesting by eumenid wasps (Collins and Jennings 1984). Danks (1971) noted that the scarcity of natural nesting sites was a limiting factor to population buildup of these wasps in England. Although strip and clearcut harvesting usually produces abundant logging slash and debris, the number of suitable nesting sites (with holes) can be increased substantially by placing predrilled blocks of wood in these open habitats.

Eumenid wasps can be trapped in one locality, transported with minimal disturbance, and released in a new locality. Such manipulations are possible because the wasps seal their nest entrances with mud. The nest remains closed until the new generation emerges. By collecting provisioned blocks before adult wasp emergence,

Summary

field crews can centrally locate wasp populations in areas of abundant prey species.

Other measures that encourage predators include lopping and scattering brush for insectivorous shrews and other small mammals (Hamilton and Cook 1940), leaving dead snags for cavity-nesting birds (Hardin and Evans 1977), and erecting shelters for bats (Buckner 1966).

In addition to environmental manipulations and cultural practices to encourage predators, curtailing the use of pesticides would help conserve natural enemies of the spruce budworm. Many parasitic and predaceous species are highly susceptible to certain pesticides; widespread use has resulted in the destruction of natural-enemy complexes (DeBach 1974, Coppel and Mertins 1977). Curtailing pesticide spraying and developing safer materials, such as insect viruses and *Bacillus thuringiensis* Berliner, will help conserve natural-enemy complexes of the spruce budworm.

We have reviewed available information on predators of the spruce budworm, their general importance in the population dynamics of the pest, methods of studying predation, and conservation and enhancement of important predators. Obviously, there are many gaps and voids in our knowledge and understanding of these agents of pest mortality. Much work remains to be done, particularly in identifying important predaceous species, determining their habitat requirements, and assessing their regulatory roles. Such information is especially needed at low population levels of the pest so that we can learn how to manage the forest to **prevent** future outbreaks. Predators definitely warrant inclusion in future pest-management systems for the spruce budworm.

Acknowledgments

We are grateful to Alison LaRochelle, Enfield, CT, for the watercolor paintings.

We thank the following for supplying information on predators: John B. Dimond, Mark W. Houseweart, Glen W. Koehler, Robert K. Lawrence, K. P. Lim, and I. W. Varty. We also thank David M. Kendall, Janet J. Melvin, Marcia A. Skratt, and Bonnie B. Grant. We are indebted to those who reviewed the manuscript: P. D. Kingsbury, Canadian Forestry Service, Forest Pest Management Institute, Sault Ste. Marie, ON; R. M. Reeves, Entomology Department, University of New Hampshire, Durham; and H. R. Smith, Northeastern Forest Experiment Station, Forest Insect and Disease Laboratory, Hamden, CT.

Verification of insect names was handled by Terry L. Erwin and Jonathan Coddington of the Department of Entomology, Smithsonian Institution; and Edward W. Baker, Robert D. Gordon, and David R. Smith of the Systematic Entomology Laboratory at the Insect Identification and Beneficial Insect Introduction Institute, USDA Agricultural Research Service. Fred Stormer, USDA Forest Service, Forest Environment Research, verified the names of birds and mammals.

Selected References and Guides for Identifying Predators

Here are general references and identification guides for various predator groups. The list is by no means exhaustive but includes books and publications that are helpful. Particularly helpful are those pertaining to introductory biologies. Most mammals and birds can be identified with field guides; identification of invertebrate predators often requires specialized keys found in taxonomic monographs. Consultation with a taxonomist or identification specialist may be advisable.

Phalangids

Bishop, S. C. The Phalangida (Opiliones) of New York with special reference to the species in the Edmund Niles Huyck Preserve, Rensselaerville, N.Y. Proceedings of the Rochester Academy of Science. 9(3): 159–235; **1949.**

Edgar, A. L. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Misc. Publ. 144. Ann Arbor, MI: University of Michigan, Museum of Zoology; **1971.** 64 p.

Spiders

Gertsch, Willis J. American spiders. 2d ed. New York: Van Nostrand Reinhold; **1979.** 274 p.

Kaston, B. J. How to know the spiders. 3d ed. The pictured key nature series. Dubuque IA: Wm. C. Brown; **1978.** 272 p.

Mites

Treat, A. E. Mites of moths and butterflies. Ithaca and London: Cornell University Press; **1975.** 362 p.

Baker, E. W.; Wharton, G. W. An introduction to Acarology. New York: Macmillan; **1952.** 465 p.

Krantz, G. W. A manual of acarology. Corvallis, OR: Oregon State University; **1978.** 509 p.

Dragonflies

Needham, J. G.; Westfall, M. J., Jr. A manual of the dragonflies of North America (Anisoptera). Berkeley and Los Angeles: University of California Press; **1955.** 615 p.

Walker, E. M. The Odonata of Canada and Alaska. Vol. 2, part III. The Anisoptera—four families. Toronto, ON: University of Toronto Press; **1958.** 318. p.

Walker, E. M.; Corbet, P. S. The Odonata of Canada and Alaska. Vol. 3, part III. The Anisoptera—three families. Toronto, ON: University of Toronto Press; **1975.** 307 p.

Carabid Beetles

Arnett, R. H., Jr. The beetles of the United States: a manual for identification. Washington, DC: Catholic University of America Press; **1963.** 1112 p.

Dillon, E. S.; Dillon, L. S. A manual of common beetles of eastern North America. Evanston, IL: Row, Peterson; **1961.** 884 p.

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 2. Opuscula Entomologica Supplementum. 20: 1–200; **1961.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 3. Opuscula Entomologica Supplementum. 24: 201–408; **1963.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 4. Opuscula Entomologica Supplementum. 29: 409–648; **1966.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 5. Opuscula Entomologica Supplementum 33: 649–944; **1968.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 6. Opuscula Entomologica Supplementum 34: 945–1192; **1969.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 1. Opuscula Entomologica Supplementum. 35: 1–48; **1969.**

Coneworms

Rose, A. H.; Lindquist, O. H. Insects of eastern spruces, fir and hemlock. For. Tech. Rep. 2. Ottawa, ON: Canadian Forestry Service; **1977.** 155 p.

Lindquist, O. H. Keys to lepidopterous larvae associated with spruce budworm in northeastern North America. Sault Ste. Marie, ON: Canadian Forestry Service, Great Lakes Forest Research Centre; **1982.** 18 p.

Robber Flies

Curran, C. H. The families and genera of North American Diptera. Mount Vernon, NY: H. Tripp; **1965.** 515 p.

Hull, F. M. Robberflies of the world. The genera of the family Asilidae. U.S. National Museum Bulletin. 224; **1962.** 907 p.

Ants

Creighton, W. S. The ants of North America. Harvard University Bulletin of the Museum of Comparative Zoology. 104; **1950.** 585 p.

Wheeler, W. M. Ants, their structure, development and behavior. New York: Columbia University Press; **1960.** 663 p.

Wasps

Evans, H. E.; Eberhard, M. J. W. The wasps. Ann Arbor, MI: University of Michigan Press; **1970.** 265 p.

Krombein, K. V. Trap-nesting wasps and bees. Washington, DC: Smithsonian Press; **1967.** 576 p.

Spradbery, J. P. Wasps. An account of the biology and natural history of social and solitary wasps. Seattle, WA: University of Washington Press; **1973.** 416 p.

Fish

Eddy, S. The freshwater fishes. Dubuque, IA: Wm. C. Brown Co.; **1969.** 286 p.

Lee, D. S.; Gilbert, C. R.; Hocutt, C. H.: Jenkins, R. E.; McAllister, D. E.; Stauffer, J. R. Atlas of North American freshwater fishes. Raleigh, NC: North Carolina Museum of Natural History; **1980.** 854 p.

Birds

Peterson, R. T. A field guide to the birds. Boston, MA: Houghton Mifflin; **1980.** 384 p.

Scott, S. L., ed. Field guide to the birds of North America. Washington, DC: National Geographic Society; **1983.** 464 p.

Mammals

Burt, W. H.; Grossenheider, R. P. A field guide to the mammals. Boston, MA: Houghton Mifflin; **1978.** 289 p.

Godin, A. J. Wild mammals of New England. Baltimore, MD: Johns Hopkins University Press; **1977.** 304 p.

Literature Cited

Akre, Roger D.; Greene, Albert; MacDonald, John F.; Landolt, Peter J.; Davis, Harry G. The yellow jackets of America north of Mexico. Agric. Handb. 552. Washington, DC: U.S. Department of Agriculture; **1980.** 102 p.

Barker, R. B.; Fyfe, H. A. A mixed infestation in the Spruce Woods Forest Reserve, Manitoba. Bimonthly Progress Report 3(4): 3; **1947.** [Ottawa, ON: Dominion Department of Agriculture, Forest Insect Investigations.]

Bell, R.; Whitcomb, W. H. *Erythemis simplicollis* (Say) a dragonfly predator of the bollworm moth. Florida Entomologist. 44: 95–97; **1961.**

Bennett, C. W. Spiders. In: Annual technical report., vol. 2, sec. 7.2. Fredericton, NB: [Canadian Department of Resources and Development], Forest Biology Laboratory; **1952a:** 305.

Bennett, C. W. Mites. In: Annual technical report., vol. 2, sec. 7.5. Fredericton, NB: [Canadian Department of Resources and Development], Forest Biology Laboratory; **1952b:** 307.

Bishop, S. C. The Phalangida (Opiliones) of New York. Proceedings of the Rochester Academy of Science. 9: 159–235; **1949.**

Blais, J. R. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research. 13: 539–547; **1983.**

Blais, J. R.; Parks, G. H. Interaction of evening grosbeak *(Hesperiphona vespertina)* and spruce budworm (*Choristoneura fumiferana* (Clem.)) in a localized budworm outbreak treated with DDT in Quebec. Canadian Journal of Zoology. 42: 1017–1024; **1964.**

Boreham, P. F. L. Recent developments in serological methods for predator–prey studies. Miscellaneous Publications of the Entomological Society of America. 11(4): 17–23; **1979.**

Borror, Donald J.; DeLong, Dwight M.; Triplehorn, Charles A. An introduction to the study of insects. 4th ed. New York: Holt, Rinehart and Winston; **1976.** 852 p.

Bruns, H. The economic importance of birds in the forest. Bird Study. 7: 193–208; **1959.**

Buckner, Charles H. The role of vertebrate predators in the biological control of forest insects. Annual Review of Entomology. 11: 449–470; **1966.**

Buckner, Charles H. Avian and mammalian predators of forest insects. Emtomophaga. 12: 491–501; **1967.**

Buckner, C. H. Vertebrate predators. In: Toward integrated control. Proceedings of the third annual northeastern forest insect work conference. Res. Pap. NE-192. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; **1971:** 21–31.

Campbell, Robert W.; Torgersen, Torolf R. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. Environmental Entomology. 11: 111–114; **1982.**

Campbell, Robert W.; Torgersen, Torolf R.; Forrest, Steven C.; Youngs, Lorna C. Bird exclosures for branches and whole trees. Gen. Tech. Rep. PNW–125. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, **1981.** 10 p.

Carter, N. E.: Brown, N. R. Seasonal abundance of certain soil arthropods in a fenitrothion-treated red spruce stand. Canadian Entomologist. 105: 1065–1073; **1973.**

Cheshire, W. F. A preliminary report on the responses of birds to the Green River spruce budworm infestations, 1949 to 1958 inclusive. Green River annual report, 1958. Fredericton, NB: Canada Department of Agriculture, Forest Biology Division; **1959.**

Clausen, C. P. Entomophagous insects. New York: McGraw-Hill; **1940.** 688 p.

Collins, Judith A.; Jennings, Daniel T. A simplified holder for eumenid nesting blocks (Hymenoptera: Eumenidae). Entomological News. 95: 58-62; **1984.**

Coppel, Harry C.; Mertins, James W. Biological insect pest suppression. Advanced series in agricultural science 4. New York:Springer-Verlag; **1977.** 314 p.

Coppel, Harry C.; Sloan, Norman F. Avian predation, an important adjunct in the suppression of larch casebearer and introduced pine sawfly populations in Wisconsin forests. In: Proceedings, Tall Timbers conference on ecological animal control by habitat management. Vol. 2; 1970 February 26–28; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station; **1971:** 259–272.

Crawford, Hewlette S.; Hooper, R. G.; Titterington, R. W. Songbird population response to silvicultural practices in central Appalachian hardwoods. Journal of Wildlife Management. 45: 680-692; **1981.**

Crawford, Hewlette S., Jr.; Jennings, Daniel T. Relationships of birds and spruce budworms—literature review and annotated bibliography. Bibliogr. Lit. Agric. 23. Washington, DC: U.S. Department of Agriculture, Forest Service, Canada/United States Spruce Budworms Program; **1982.** 40 p.

Crawford, Hewlette S.; Titterington, Richard W. Effects of silvicultural practices on bird communities in upland spruce–fir stands. In: Management of northcentral and northeastern forests for nongame birds: proceedings of the workshop; 1979 January 23–25; Minneapolis, MN. Gen. Tech. Rep. NC-51. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station; **1979:** 110–119.

Crawford, H. S.; Titterington, R. W.; Jennings, D. T. Bird predation and spruce budworm populations. Journal of Forestry. 81: 433–435; **1983.**

Danks, H. V. Biology of some stem-nesting aculeate Hymenoptera. Transactions of the Royal Entomological Society of London. 122: 323–395; **1971.**

DeBach, P. Biological control by natural enemies. London–New York: Cambridge University Press; **1974.** 323 p.

DeBach, P.; Bartlett, B. R. Methods of colonization, recovery and evaluation. In: DeBach, P., ed. Biological control of insect pests and weeds. New York: Reinhold; **1964:** 402–426.

DeBach, Paul; Huffaker, C. B.; MacPhee, A. W. Evaluation of the impact of natural enemies. In: Huffaker, C. B.; Messenger, F. S., eds. Theory and practice of biological control. New York: Academic Press; **1976:** 255–285.

Dempster, J. P. A quantitative study of the predators on the eggs and larvae of the broom beetle, *Phytodecta olivacea* Forester, using the precipitin test. Journal of Animal Ecology. 29: 149–167; **1960.**

Doganlar, Miktat; Beirne, Bryan P. Natural enemies of budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), on Douglas-fir near Yale, British Columbia, in 1977. Journal of the Entomological Society of British Columbia. 75: 25–26; **1978.**

Dominion Department of Agriculture. Annual technical report. Vol. 2. Fredericton, NB: Dominion Department of Agriculture, Forest Insect Investigations, Dominion Entomological Laboratory; **1950.** 556 p.

Dowden, Philip B.; Carolin, V. M.; Dirks, C. O. Natural control factors affecting the spruce budworm in the Adirondacks during 1946–1948. Journal of Economic Entomology. 43: 774–783; **1950.**

Dowden, Philip B.; Jaynes, H. A.; Carolin, V. M. The role of birds in a spruce budworm outbreak in Maine. Journal of Economic Entomology. 46: 307–312; **1953.**

Edgar, A. L. Studies on the biology and ecology of Michigan phalangida (Opiliones). Misc. Publ. 144. Ann Arbor, MI: University of Michigan, Museum of Zoology; **1971.** 64 p.

Finnegan, R. J. An appraisal of indigenous ants as limiting agents of forest pests in Quebec. Canadian Entomologist. 103: 1489–1493; **1971.**

Finnegan, R. J. Ants as predators of forest pests. Entomophaga. 7: 53–59; **1974.**

Finnegan, R. J. Introduction of a predaceous red wood ant, *Formica lugubris* (Hymenoptera: Formicidae), from Italy to eastern Canada. Canadian Entomologist. 107: 1271–1274; **1975.**

Finnegan, R. J. Establishment of a predaceous red wood ant, *Formica obscuripes* (Hymenoptera: Formicidae), from Manitoba to eastern Canada. Canadian Entomologist. 109: 1145–1148; **1977.**

Finnegan, R. J. Predation by *Formica lugubris* (Hymenoptera: Formicidae) on *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Bi-monthly Research Notes. 34(1): 3–4; **1978.** [Ottawa, ON: Fisheries and Environment Canada, Canadian Forestry Service.]

Francoeur, A. Formicoidea. In: Danks, H. V., ed. Canada and its insect fauna. Memoirs of the Entomological Society of Canada. 108: 502–503; **1979.**

Franz, J. M. Biological control of pest insects in Europe. Annual Review of Entomology. 6: 183–200; **1961.**

Freitag, R.; Ozburn, G. W.; Leech, R. E. The effects of sumithion and phosphamidon on populations of five carabid beetles and the spider *Trochosa terricola* in northwestern Ontario, including a list of collected species of carabid beetles and spiders. Canadian Entomologist. 101: 1328–1333; **1969.**

Freitag, R.; Poulter, F. The effects of the insecticides sumithion and phosphamidon on populations of five species of carabid beetles and two species of lycosid spiders in northwestern Ontario. Canadian Entomologist. 102: 1307–1311; **1970.**

Fye, R. E. Predation of lepidopterous larvae by solitary wasps. Bi-monthly Progress Reports. 18(2): 2–3; **1962.** [Ottawa, ON: Canadian Department of Forestry, Forest Entomology and Pathology Branch.]

Fye, R. E. The biology of the Vespidae, Pompilidae, and Sphecidae (Hymenoptera) from trap nests in northwestern Ontario. Canadian Entomologist. 97(7): 716–744; **1965.**

Fye, R. E. The effect of forest disturbances on populations of wasps and bees in northwestern Ontario (Hymenoptera: Aculeata). Canadian Entomologist. 104: 1623–1633; **1972.**

Gage, S. H.; Miller, C. A. A long-term bird census in spruce budworm-prone balsam fir habitats in northwestern New Brunswick. Inf. Rep. M-X-84. Fredericton, NB: Department of Fisheries and the Environment, Canadian Forestry Service; **1978.** 6 p.

Gage, S. H.; Miller, C. A.; Mook, L. J. The feeding response of some forest birds to the black-headed budworm. Canadian Journal of Zoology. 48: 359–366; **1970.**

George, John L.; Mitchell, Robert T. Calculations on the extent of spruce budworm control by insectivorous birds. Journal of Forestry. 46: 454–455; **1948.**

Gidaspow, T. North American caterpillar hunters of the genera *Calosoma* and *Callisthenes* (Coleoptera: Carabidae). Bulletin of the American Museum of Natural History. 116: 225–344; **1959.**

Glen, R. Factors that affect insect abundance. Journal of Economic Entomology. 47: 398–405; **1954.**

Graham, S. A.; Orr, L. W. The spruce budworm in Minnesota. Tech. Bull. 142. St. Paul, MN: University of Minnesota Agricultural Experiment Station; **1940.** 27 p.

Greenbank, D. O. The analysis of moth survival and dispersal in the unsprayed area. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 87–99; **1963.**

Hamilton, W. J., Jr.; Cook, David B. Small mammals and the forest. Journal of Forestry. 38: 468–477; **1940.**

Hardin, Kimberly I.; Evans, Keith E. Cavity nesting bird habitat in the oak–hickory forest—a review. Gen. Tech. Rep. NC-30. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station; **1977.** 23 p.

Haynes, Dean L.; Sisojevic, P. The predatory behavior of *Grammonota angusta* Dondale (Araneae: Erigonidae). Intern. Rep. M-15. Fredericton, NB: Canadian Department of Forestry, Forest Research Laboratory; **1966.** 42 p.

Hirtle, F. C. Studies on the bionomics and natural control of the spruce budworm, (*Choristoneura fumiferana* (Clem.)), in the Green River watershed, N.B. In: Annual technical report, vol. 3, sec. 4. Fredericton, NB: [Canadian Forestry Service], Forest Insect Investigations; **1951:** 142–161.

Holling, C. S. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist. 91: 293–320; **1959a.**

Holling, C. S. Some characteristics of simple types of predation and parasitism. Canadian Entomologist. 91: 385–398; **1959b.**

Holling, C. S. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada. 48: 1–86; **1966.**

Holling, C. S.; Buckingham, S. A behavioral model of predator–prey functional responses. Behavioral Science. 21: 183–195; **1976.**

Houseweart, Mark W.; Jennings, Daniel T.; Berkett, Lorraine P.; Brann, Thomas B. Parasitic mites (Acari: Erythraeidae) on spruce budworm moths (Lepidoptera: Tortricidae). Canadian Entomologist. 112: 193–197; **1980.**

Houseweart, Mark W.; Southard, Susan G.; Jennings, Daniel T. Availability and acceptability of spruce budworm eggs to parasitism by the egg parasitoid *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). Canadian Entomologist. 114: 657–666; **1982.**

Hydorn, Susan B.; Rabeni, Charles F.; Jennings, Daniel T. Effects of forest spraying with acephate insecticide on consumption of spiders by brook trout *(Salvelinus fontinalis).* Canadian Entomologist. 111: 1185–1192; **1979.**

Jaynes, H. A.; Speers, C. F. Biological and ecological studies of the spruce budworm. Journal of Economic Entomology. 42: 221–225; **1949.**

Jennings, Daniel T. Ants preying on dislodged jack-pine budworm larvae. Annals of the Entomological Society of America. 64: 384–385; **1971.**

Jennings, Daniel T.; Crawford, Hewlette S. Pine siskin preys on egg masses of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist. 115: 439–440; **1983.**

Jennings, Daniel T.; Houseweart, Mark W. Spider preys on spruce budworm egg mass. Entomological News. 89: 183–186; **1978.**

Jennings, Daniel T.; Houseweart, Mark W. Predation by eumenid wasps (Hymenoptera: Eumenidae) on spruce budworm (Lepidoptera: Tortricidae) and other lepidopterous larvae in spruce–fir forests of Maine. Annals of the Entomological Society of America. 77: 39–45; **1984.**

Jennings, Daniel T.; Houseweart, Mark W.; Cokendolpher, James C. Phalangids (Arachnida: Opiliones) associated with strip clearcut and dense spruce–fir forests of Maine. Environmental Entomology. 13: 1306–1311; **1984.**

Jennings, Daniel T.; Houseweart, Mark W.; Dimond, John B. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce–fir forests of Maine. Environmental Entomology. 12: 1787–1792; **1983.**

Johannsen, O. A. Spruce bud-worm *(Tortrix fumiferana, Clemens).* Bull. 210. Orono, ME: Maine Life Sciences Agricultural Experiment Station; **1913.** 31 p.

Johnson, Norman E.; Cameron, R. Scott. Phytophagous ground beetles. Annals of the Entomological Society of America. 62: 909–914; **1969.**

Kendeigh, S. Charles. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Biol. Bull. 1. Ontario, Canada: Department of Lands and Forests, Division of Research; **1947.** 100 p.

Kingsbury, P. D.; Kreutzweiser, D. P. Dosage-effect studies on the impact of permethrin on trout streams. Rep. FPM-X-31. Sault Ste. Marie, ON: Department of the Environment, Canadian Forestry Service, Forest Pest Management Institute; **1980.** 51 p.

Kiritani, K.; Dempster, J. P. Different approaches to the quantitative evaluation of natural enemies. Journal of Applied Ecology. 10: 323–330; **1973.**

Kirkton, Rodney M. Habitat management and its effects on populations of *Polistes* and *Iridomyrmex.* In: Proceedings, Tall Timbers conference on ecological animal control by habitat management. Vol. 2; 1970 February 26–28; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station; **1971:** 243–246.

Korschgen, Leroy J. Proceedings for food-habits analyses. In: Schemnitz, Sanford D., ed. Wildlife management techniques manual. 4th ed., rev. Washington, DC: Wildlife Society; **1980:** 113–127.

Krall, Jay H. The predation of litter-dwelling carabidae on larvae of the spruce budworm, *Choristoneura fumiferana,* in northern Maine. Orono, ME: University of Maine; **1977.** 92 p. M.S. thesis.

Krall, J. H.; Simmons, Gary A. Tree root injection of phosphorus-32 for labeling defoliating insects. Environmental Entomology. 6: 159–160; **1977.**

Krombein, Karl V. Trap-nesting wasps and bees: life histories, nests, and associates. Washington, DC: Smithso nian Press; **1967.** 570 p.

Krombein, Karl V.; Hurd, Paul D., Jr.; Smith, David R.; Burks, B. D. Catalog of Hymenoptera in America north of Mexico. Vol. 2: Apocrita (Aculeata). Washington, DC: Smithsonian Institution Press; **1979:** 1472–1510.

Kulman, H. M. Comparative ecology of North American Carabidae with special reference to biological control (1). Entomophaga. 7: 61–70; **1974.**

Lawson, F. R.; Rabb, R. L.; Guthrie, F. E.; Bowery, T. G. Studies of an integrated control system for hornworms on tobacco. Journal of Economic Entomology. 54: 93–97; **1961.**

Leius, K. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. Canadian Entomologist. 92: 369–376; **1960.**

Lindroth, C. H. The ground beetles of Canada and Alaska. Part 1. Opuscula Entomologica Supplementum. 35: 1–48; **1969.**

Liscombe, E. A. R.; Lejeune, R. R. Natural control of the spruce budworm. Bimonthly Progress Reports 5(6): 2; **1949.** [Ottawa, ON: Dominion Department of Agriculture, Science Service, Division of Entomology, Forest Insect Investigations.]

Loughton, B. G.; Derry, C.; West, A. S. Spiders and the spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 249–268; **1963.**

Macdonald, D. R.; Webb, F. E. Insecticides and the spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 228–310; **1963.**

MacKay, Margaret R. The spruce foliage worm and the spruce cone worm (*Dioryctria* spp., Lepidoptera, Pyralidae). Canadian Entomologist. 75: 91–98; **1943.**

McIver, James D. An examination of the utility of the precipitin test for evaluation of arthropod predator–prey relationships. Canadian Entomologist. 113: 213–222; **1981.**

McLeod, J. M.; Daviault, L. Notes on the life history and habits of the spruce cone worm, *Dioryctria reniculella* (Grt.) (Lepidoptera: Pyralidae). Canadian Entomologist. 95: 309–316; **1963.**

McNeil, Jeremy N.; Delisle, Johanne; Finnegan, R. J. Seasonal predatory activity of the introduced red wood ant, *Formica lugubris* (Hymenoptera: Formicidae) at Valcartier, Quebec, in 1976. Canadian Entomologist. 110: 85–90; **1978.**

Medler, J. T.; Fye, R. E. Biology of *Ancistrocerus antilope* (Panzer) (Hymenoptera, Vespidae) in trap-nests in Wisconsin. Annals of the Entomological Society of America. 49(1): 97–102; **1956.**

Medler, J. T.; Koerber, T. Biology of *Dipogon sayi sayi* Banks in trap nests in Wisconsin. Annals of the Entomological Society of America. 50: 621–625; **1957.**

Miller, C. A. The measurement of spruce budworm populations and mortality during the first and second larval instars. Canadian Journal of Zoology. 36: 409–422; **1958.**

Miller, C. A. The spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 12–19; **1963a.**

Miller, C. A. The analysis of pupal survival in the unsprayed area. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 63–70; **1963b.**

Miller, C. A.; Varty, I. W. Biological methods of spruce budworm control. In: The spruce budworm. Forestry Chronicle. 51: 150–153; **1975.**

Miller, M. C. Preparatory im munodiffusion for production of specific anti-adult southern pine beetle serum. Annals of the Entomological Society of America. 72: 820–825; **1979.**

Mitchell, Robert T. Consumption of spruce budworms by birds in a Maine spruce–fir forest. Journal of Forestry. 50: 387–389; **1952.**

Mook, L. J. Birds and the spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 268–271; **1963.**

Morimoto, R. *Polistes* wasps as natural enemies of agricultural and forest pests. 1. Studies on the social Hymenoptera of Japan 10. Science Bulletin of the Faculty of Agriculture, Kyushu University. 18: 110–116; **1960.**

Morris, R. F. Green River Project—summary of entomological investigations in 1947. Bimonthly Progress Reports. 4(1): 1–2; **1948.** [Ottawa, ON: Dominion Department of Agriculture, Science Service—Division of Entomology, Forest Insect Investigations.]

Morris, R. F. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Canadian Journal of Zoology. 33: 107–223; **1955.**

Morris, R. F. Predation and the spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 244–248; **1963.**

Morris, R. F.; Cheshire, W. F.; Miller, C. A.; Mott, D. G. The numerical response of avian and mammalian predators during a graduation of the spruce budworm. Ecology. 39: 487–494; **1958.**

Morris, R. F.; Mott, D. G. Dispersal and the spruce budworm. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 180–189; **1963.**

Mott, D. G. The analysis of the survival of small larvae in the unsprayed area. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 42–52; **1963.**

Neilson, M. M. The analysis of egg survival in the unsprayed area. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 37–41; **1963.**

Nicholson, A. J. The balance of animal populations. Journal of Animal Ecology. 2 (Supplement 1): 132–178; **1933.**

Nicholson, A. J. An outline of the dynamics of animal populations. Australian Journal of Zoology. 2: 9–65; **1954.**

Odum, E. P.; Golley, F. B. Radioactive tracers as an aid to the measurement of energy flow at the population level in nature. In: Schultz, V.; Klement, A. W., eds. Radioecology. New York: Rheinhold Publ. Corp.; **1963:** 403–410.

Otvos, I. S. Predators. In: Hudak, J.; Raske, A. G., eds. Review of the spruce budworm outbreak in Newfoundland—its control and forest management implications. Inf. Rep. N-X-205. St. John's, NF: Environment Canada, Canadian Forestry Service; **1981:** 103–104.

Price, Peter W. Insect ecology. New York: John Wiley & Sons; **1975.** 514 p.

Reeves, R. Marcel; Dunn, Gary A.; Jennings, Daniel T. Carabid beetles (Coleoptera: Carabidae) associated with the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist. 115: 453–472; **1983.**

Renault, T. R.; Miller, C. A. Spiders in a fir–spruce biotype: abundance, diversity, and influence on spruce budworm densities. Canadian Journal of Zoology. 50: 1039–1046; **1972.**

Rose, A. H.; Lindquist, O. H. Insects of eastern spruces, fir and hemlock. For. Tech. Rep. 23. Ottawa, ON: Department of the Environment, Canadian Forestry Service; **1977.** 159 p.

Royama, T. A comparative study of models for predation and parasitism. Researches on Population Ecology. 13 (Supplement 1): 1–91; **1971**

Royama, T. Population persistence and density dependence. Ecological Monographs. 47(1): [reprint p. 1–35]; **1977.**

Sailer, R. I. Invertebrate predators. In: Toward integrated control. Proceedings of the third annual northeastern forest insect work conference. Res. Pap. NE-94. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; **1971:** 32–44.

Sanders, C. J., comp. A summary of current techniques used for sampling spruce budworm populations and estimating defoliation in eastern Canada. Rep. O-X-306. Sault Ste. Marie, ON: Department of the Environment, Canadian Forestry Service, Great Lakes Forest Research Centre; **1980.** 33 p.

Sanders, C. J.; van Frankenhuyzen, K. High populations of a carabid beetle associated with spruce budworm. Bi-monthly Research Notes. 35(4): 21–22; **1979.** [Ottawa, ON: Environment Canada, Canadian Forestry Service.]

Smith, B. C. Variation in weight, size, and sex ratio of coccinellid adults (Coleoptera: Coccinellidae). Canadian Entomologist. 98: 639–644; **1966.**

Solomon, M. E. The natural control of animal populations. Journal of Animal Ecology. 18: 1–35; **1949.**

Southwood, T. R. E. Ecological methods, with particular reference to the study of insect populations. 2d ed., rev. London: Chapman and Hall; **1978.** 524 p.

Stern, Vernon M.; Adkisson, Perry L.; Beingolea, Oscar G.; Viktorov, G. A. Cultural controls. In: Huffaker, C. B.; Messenger, P. S., eds. Theory and practice of biological control. New York: Academic Press; **1976:** 593–613.

Syme, P. D. The effect of wild carrot on a common parasite of the European pine shoot moth. Bimonthly Research Notes. 22(4): 3; **1966.** [Ottawa, ON: Canadian Department of Forestry.]

Syme, P. D. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. Environmental Entomology. 4: 337–346; **1975.**

Thomson, H. M. A note on the predation of spruce budworm pupae. Bi-monthly Progress Reports. 13(4): 2; **1957.** [Ottawa, ON: Canadian Department of Agriculture, Science Service, Forest Biology Division.]

Tinbergen, L. The natural control of insects in pinewoods. 1. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie. 13: 265–336; **1960.**

Titterington, R. W.; Crawford, H. S.; Burgason, B. N. Songbird responses to commercial clear-cutting in Maine spruce–fir forests. Journal of Wildlife Management. 43: 602–609; **1979.**

Todd, Valerie. Prey of harvestmen (Arachnida, Opiliones). The Entomologist's Monthly Magazine. 86: 252–254; **1950.**

Tothill, J. D. Notes on the outbreaks of spruce budworm, forest tent caterpillar, and larch sawfly in New Brunswick. Proceedings of the Acadian Entomological Society. 8: 172–182; **1923.**

Treat, Asher E. Mites of moths and butterflies. Ithaca and London: Cornell University Press; **1975.** 362 p.

Tsomides, Leonidas; Gibbs, K. Elizabeth; Jennings, Daniel T. Species of Odonata feeding on Lepidoptera in spruce–fir forests of Maine. Research in the Life Sciences. 39(1): 1–12; **1982.** Orono, ME: University of Maine, Life Sciences and Agriculture Experiment Station.

Turnbull, A. L. Spider predators of the spruce budworm, *Choristoneura fumiferana* (Clem.), at Lillooet, B.C., Canada. Vol. 3A. Proceedings of the Eighth Pacific Science Congress, **1956:** 1579–1593.

Turnbull, A. L. The prey of the spider *Linyphia triangularis* (Clerck), (Araneae, Linyphiidae). Canadian Journal of Zoology. 38: 859–873; **1960.**

Varty, I. W. Ecology of *Mulsantina hudsonica* Casey, a ladybeetle in fir–spruce forest. Intern. Rep. M-42. Fredericton, NB: Canadian Department of Fisheries and Forestry, Forestry Branch; **1969.** 28 p.

Varty, I. W. Long-term effects of fenitrothion spray programs on non-target terrestrial arthropods. Proceedings of the symposium on fenitrothion; 1977 April 20–22. Ottawa, ON: National Research Council Canada; **1977:** 343–375.

Varty, I. W. Forest tree insects and spiders. In: Environmental surveillance in New Brunswick, 1978–1979, effects of spray operations for forest protection against spruce budworm. Fredericton, NB: Department of Forest Resources, University of New Brunswick; **1980:** 44–46.

Varty, I. W.; Carter, N. E. A baseline inventory of litter-dwelling arthropods and airborne insects including pollinators in two fir–spruce stands with dissimilar histories of insecticide treatment. Inf. Rep. M-X-48. Fredericton, NB: Department of the Environment, Canadian Forestry Service, Maritimes Forest Research Centre; **1974.** 32 p.

Varty, I. W.; Titus, F. A. Effects of phosphamidon sprays on non-target insects in fir–spruce forest, spruce budworm adulticide trials 1973. Inf. Rep. M-X-47. Fredericton, NB: Department of the Environment, Canadian Forestry Service, Maritimes Forest Research Centre; **1974.** 24 p.

Warren, G. L. The spruce needleworm, *Dioryctria reniculella* Grt., as a predator of spruce budworm. Bi-monthly Progress Reports. 10(3): 2–3; **1954.** [Ottawa, ON: Canadian Department of Agriculture, Science Service, Forest Biology Division.]

Watt, K. E. F. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. Canadian Entomologist. 91: 129–144; **1959.**

Watt, K. E. F. The analysis of the survival of large larvae in the unsprayed area. In: Morris, R. F., ed. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada. 31: 52–63; **1963.**

Zach, Reto; Falls, J. Bruce. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. Canadian Journal of Zoology. 53: 1669–1672; **1975.**